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MADROÑO

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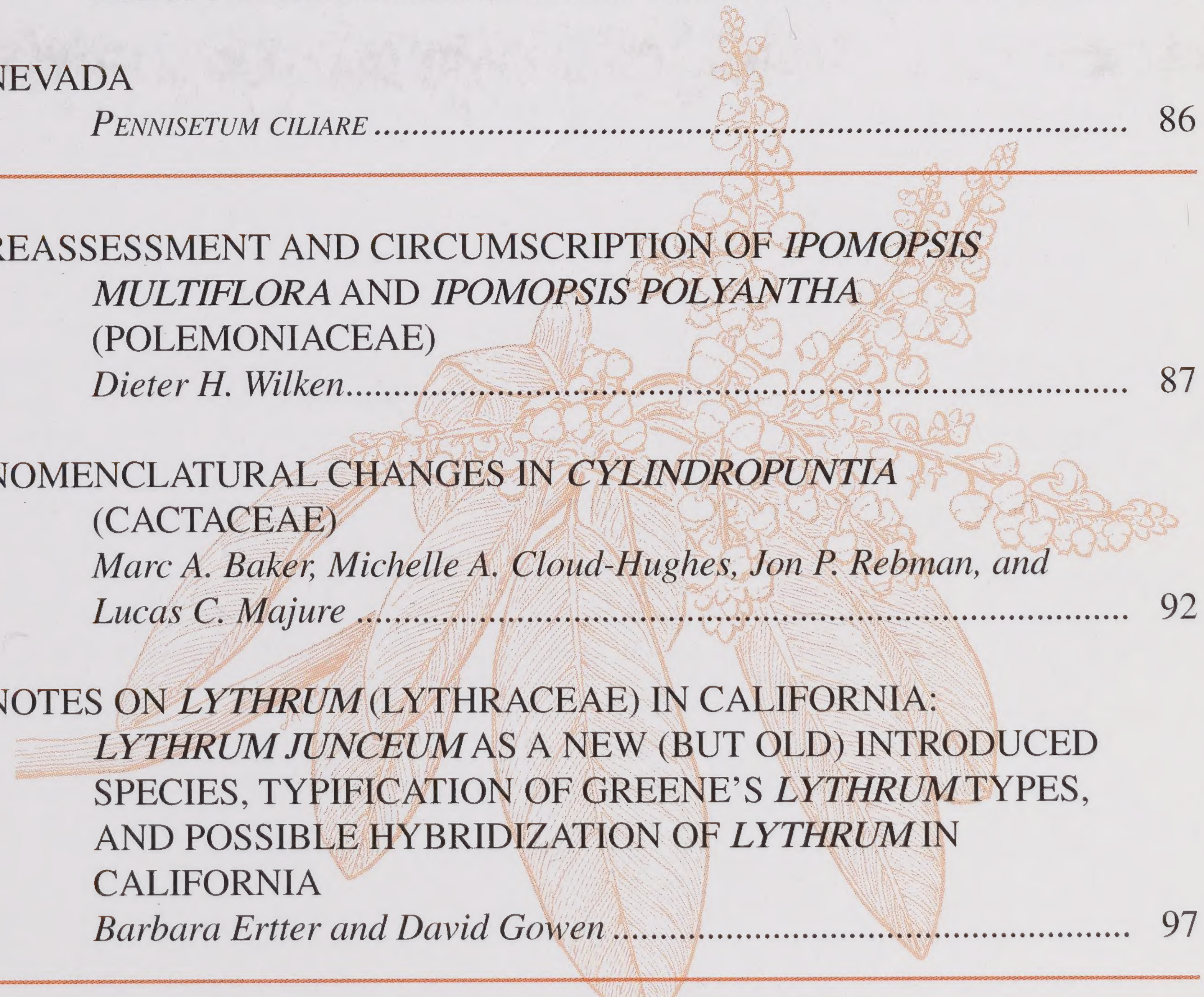

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MADROÑO, Vol. 66, No. 3, p. 85, 2019

NOTEWORTHY COLLECTION

CALIFORNIA

ISOETES ORCUTTII A.A.Eaton (ISOETACEAE).—Los Angeles Co., San Clemente Island, SHOBA (Shore Bombardment Area), NE side of Guds Mountain, 32.830423°, –118.366734°, 235 m, 20 March 2019, *J. Rebman 35341* (SD). Approximately 50 plants, on clayey soils in open areas. Associated species include: *Acmispon argophyllus* (A.Gray) Brouillet var. *argenteus* (Dunkle) Brouillet, *Bromus diandrus* Roth, *Calystegia macrostegia* (Greene) Brummitt subsp. *amplissima* Brummitt, *Crassula connata* (Ruiz & Pav.) A.Berger, *Cylindropuntia prolifera* (Engelm.) F.M.Knuth, *Lasthenia gracilis* (DC.) Greene, *Opuntia littoralis* (Engelm.) Cockerell, *Plantago erecta* E.Morris, *Trifolium depauperatum* Desv., and *Trifolium willdenovii* Spreng.

Previous knowledge. *Isoetes orcuttii* had been known from southwestern Oregon to northwestern Baja California, but only on the mainland (Taylor and Keeley 2012). The Jepson Manual lists this taxon as a vernal pool species (Taylor and Keeley 2012), yet this collection was made on a moist slope, with no obvious proximity to vernal pool habitat. It was not known from the California Channel Islands (Ratay et al. 2014). It is not currently considered a species of conservation concern (CNPS 2019).

Significance. This collection extends the range of *Isoetes orcuttii* to the California Channel Islands, adding a new species, genus, and family to the archipelago (including the Baja California Pacific Islands).

—JON REBMAN AND SULA VANDERPLANK, San Diego Natural History Museum, 1788 El Prado, San Diego, CA 92101. jrebman@sdnhm.org; KIMBERLY O'CONNOR, U.S. Pacific Fleet, U.S. Department of the Navy, 3455 Senn St., San Diego, CA, 92136; BRYAN MUNSON, Naval Base Coronado, U.S. Department of the Navy, 3632 Tulagi Rd., Coronado, CA, 92118.

ACKNOWLEDGMENTS

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MADROÑO, Vol. 66, No. 3, p. 86, 2019

NOTEWORTHY COLLECTIONS

NEVADA

PENNISETUM CILIARE (L.) Link (POACEAE).—Clark County, Eldorado Valley, along the Eldorado-Ivanpah Transmission Project power line, 35.759667°, −115.100217° (UTM Z11 0671751E, 3958957N) (NAD83), with *Atriplex canescens* (Pursh) Nutt., *Encelia farinosa* A.Gray ex Torr., *Larrea tridentata* (Sessé & Moc. ex DC.) Coville, *Schismus* sp., and *Sphaeralcea ambigua* A.Gray, 720 m, 2 mature plants found in a revegetated area, 11 May 2018, *T. Embrey 201 with R. Crawford* (ARIZ, RENO). After we collected voucher specimens, the plants were dug up and burned.

Previous knowledge. The closest known collections are from the Burro Creek area of Mohave County, Arizona (*Anderson 2015-04*), and near Twentynine Palms, San Bernardino County, California (*Harding & Hoines 38*), roughly 185 and 204 kilometers away, respectively (Consortium of California Herbaria 2019; SEINet 2019). Both labels state that these colonies were extirpated on the day of collection.

The presence of buffelgrass in Nevada has been known since at least 2014, from an unvouchered occurrence near Laughlin. The Exotic Plant Management Team, based at Lake Mead National Recreation Area, detected plants at the Colorado River Heritage Greenway Park and Trails area, along the paved path from the picnic area to the river. This initial occurrence of 10 mature plants and 150 seedlings were chemically treated, and current efforts are confined to fighting the seed bank (C. Norman, National Park Service, personal communication).

Significance. This represents the northernmost collection in the United States for this taxon, and a first to the flora of Nevada (Kartesz 1987; SEINet 2019; K. Birgy, University of Nevada Las Vegas, personal communication). Native to the Old World, this plant is considered a noxious weed in Arizona, and has significantly altered the landscape in parts of the southwestern United States and Mexico (Van Devender and Dimmit 2006; Arizona Department of Agriculture 2019).

At both Nevada locations, it appears that plants were unintentionally introduced, either via heavy-duty machinery or as part of landscaping efforts.

Pennisetum ciliare currently has no status in Nevada (Nevada Department of Agriculture 2019). I recommend that it be added to weed watch lists for Clark County, Nevada, and, due to the vicinity, neighboring areas in California.

—TEAGUE EMBREY, 220 W. Franklin St., Tucson, AZ 85701; teague84@hotmail.com

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MADROÑO, Vol. 66, No. 3, pp. 87–91, 2019

REASSESSMENT AND CIRCUMSCRIPTION OF *IPOMOPSIS MULTIFLORA* AND *IPOMOPSIS POLYANTHA* (POLEMONIACEAE)

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ABSTRACT

Two infraspecific taxa previously treated as varieties of *Gilia polyantha* Rydb. are recognized as belonging to *Ipomopsis multiflora* (Nuttall) V.E.Grant, which requires lectotypification. The new combinations, *Ipomopsis multiflora* (Nuttall) V.E.Grant subsp. *brachysiphon* (Wooton & Standley) Wilken, *comb. & stat. nov.* and subsp. *whitingii* (Kearney & Peebles) Wilken, *comb. & stat. nov.* are necessary for the treatment of *Ipomopsis* in a forthcoming volume of the Flora North America North of Mexico.

Key Words: *Ipomopsis multiflora*, *Ipomopsis polyantha*, Polemoniaceae.

Ipomopsis multiflora (Nuttall) V.E.Grant and *Ipomopsis polyantha* (Rydberg) V.E.Grant, are collectively characterized as short-lived perennials with simple to pinnatifid cauline leaves, a thyrsate, secund inflorescence, puberulent calyx tubes, salverform corollas with white to violet, elliptic to ovate corolla lobes, exserted styles, and exserted stamens inserted in the upper throat just below the sinuses. *Ipomopsis polyantha* is a narrow endemic, restricted to the Mancos Shale formation of Archuleta County, Colorado (Ackerfield 2015) and is listed as Endangered by the U.S. Fish and Wildlife Service (Ashe 2011). In contrast, *Ipomopsis multiflora* is widespread in southern Colorado, New Mexico, and Arizona (Kearney and Peebles 1960; MacDougall 1973; Martin and Hutchins 1981; Wilken and Porter 2005; Ackerfield 2015). Originally treated as part of *Gilia*, the two species are included in *Ipomopsis*, which is circumscribed based on leaf and floral morphology, base chromosome number ($n = 7$), and several phylogenetic studies (Porter and Johnson 2000; Porter et al. 2010).

Kearney and Peebles (1943) recognized *Gilia multiflora* Nutt. and *Gilia polyantha* Rydb., separating them primarily on differences in corolla tube length and corolla lobe shape. They also recognized two varieties of *Gilia polyantha* as distinct from typical *polyantha:* var. *brachysiphon* (Woot. & Standl.) Kearney & Peebles, and var. *whitingii* Kearney & Peebles. The differences among the three varieties were based primarily on the color of the corolla lobes, corolla lobe shape and size, and distal stem indumentum.

Notably, Cronquist (1984) recognized the same three varieties, but described var. *whitingii* as having flowers with "slightly irregular" corollas with three lobes "forming a sort of lower lip" and prominently "exserted, upturned" (declinate) staminal filaments. Unfortunately, this contrasts with the illustration of *Gilia polyantha* var. *whitingii* (Cronquist 1984, p. 125), which shows a flower with a short corolla tube, lobes equal in length, and straight stamens. Martin and Hutchins (1981) treated *Gilia brachysiphon* Wooton & Standley as a synonym of *Ipomopsis multiflora*, which they described as having "conspicuously exserted, declined" stamens, and reported *Ipomopsis polyantha* as occurring in New Mexico.

Phylogenetic relationships remain unresolved using molecular data. Chloroplast (*trnL-F*) and nuclear (ITS) DNA sequence data suggest that *Ipomopsis multiflora*, *Ipomopsis polyantha*, and *Gilia polyantha* subsp. *whitingii* may be derived from different ancestors within *Ipomopsis* (Porter et al. 2010). Another analysis, using plastid genes, revealed an unresolved clade composed of typical *I. multiflora*, typical *I. polyantha*, *Ipomopsis longiflora* (Torr.) V.E.Grant, and *Ipomopsis aggregata* subsp. *bridgesii* (A.Gray) V.E.Grant & A.D.Grant (Landis et al. 2018). Unfortunately, *Gilia polyantha* subsp. *whitingii* was not included in their study.

Studies of morphological variation over a broad area of New Mexico and Arizona, summarized in Wilken and Porter (2005) and Porter (2013), suggested that var. *whitingii* is more closely related to *Ipomopsis multiflora*. Subsequent studies also revealed a similar relationship between var. *brachysiphon* and *Ipomopsis multiflora*. Thus, based on morphological evidence summarized here from observations in the field and herbarium specimens, the two varieties are more closely related to *Ipomopsis multiflora*, with which they share violet to lavender corollas, elliptic to oblong or obovate corolla lobes, calyx lobe mucros 0.3–1.3 mm long, and simple or 2–3-pinnate mid-cauline leaves. The proposed combinations are necessary for a treatment of *Ipomopsis* in a forthcoming volume of the Flora of North America North of Mexico.

The length of the corolla tube was measured to the nearest 0.5 mm from the base of the corolla tube at its insertion adjacent to the ovary to the base of the corolla lobes and includes the slightly expanded throat below the sinuses between the lobes.

TAXONOMY

Ipomopsis polyantha (Rydb.) V.E.Grant, El Aliso 3:357. 1956. Basionym: *Gilia polyantha* Rydb., Bull. Torrey Bot. Club 31:634. 1904. *Gilia multiflora* Nutt. var. *polyantha* (Rydb.) Brand, Pflanzenr. (Engler) 4, Fam. 250:113. 1907—HOLOTYPE: USA. Colorado. Archuleta Co.: Pagosa Springs, Jul 28, 1899, *C.F. Baker 538* (NY!). *Gilia exserta* A.Nelson, Bot. Gaz. 40: 65. 1905 —HOLOTYPE: USA. Colorado. Archuleta Co.: Pagosa Springs, Jul 28, 1899, *C.F. Baker* 538 (RM!).

Gilia polyantha Rydb. and *Gilia exserta* A.Nelson are based on specimens from the same gathering (Baker 538). There is no evidence that *Ipomopsis polyantha* occurs in New Mexico (Ashe 2011; SEINET 2019).

Diagnostic description. Flowering stems 31–55 cm, erect, densely glandular- and eglandular-puberulent, sparsely villosulous. Mid-cauline leaves 2–3.3 cm, pinnatifid, the lobes 3–5, 5–10 mm long, sparsely glandular and eglandular-puberulent. Inflorescence branches each with 5–9 flowers. Calyx lobe mucros 0.1–0.5 mm. Corolla radial, tube and throat white to faintly bluish, 4.5–7 mm long; throat 1.5–3 mm wide; lobes white or faintly bluish, with pink to violet flecks, widely elliptic to ovate, equal in length and shape, 3.5–5 mm long, 2–3 mm wide, apices acute to apiculate. Staminal filaments equal, straight, 5–8 mm; anthers strongly exserted; styles 6–9 mm.

Representative specimens: USA. COLORADO. **Archuleta Co.**: Pagosa Springs, 30 Jun 1921, *Bethel, Willey, and Clokey 4251* (CAS, COLO); 2 mi E of Pagosa Springs, 27 Aug 1946, *Parker 6430* (CAS); 1 mi SE of Pagosa Springs, 14 Jun 1967, *Harrington 9981* (CS); 0.2 mi E of Dyke, 5 Jun 1985, *O'Kane 2077* (CS); 2 mi SE of Pagosa Springs, Jul 5, 1954, *Ripley and Barneby 10284* (CAS, NY); SE of Pagosa Springs on road to Chromo, 20 Jun 1951, *Weber and Livingston 6334* (CAS, COLO, CS, RM).

Ipomopsis multiflora (Nutt.) V.E.Grant, El Aliso 3:357. 1956. Basionym: *Gilia multiflora* Nutt. Proc. Acad. Nat. Sci. Philadelphia iv. 1848; Journ. Acad. Nat. Sci. Philad., Ser. 2, i. 154. 1848. Lectotype (here designated) —USA. New Mexico: Rio del Norte, 1841, *Gambel* (GH, Image seen, GH 78887). Syntype —Sta Feé [Santa Fe], *Gambel* (K. image seen, K 769149).

The lectotypification proposed here is based on an examination of syntypes at GH and K, assumed to be collected by William Gambel and which are presumably duplicates of the original specimen studied by Thomas Nuttall (1848). Following his temporary return to the United States in 1847–1848, Nuttall worked on a publication of new taxa based on specimens collected in 1841 by Gambel (Reveal and Spevak 1967; Jercinovic 2004). However, no Gambel collections could be found at PH. The specimen at GH bears a printed label that reads "ex Herb. John A. Lowell. Transferred from The Boston Society of Natural History to the Gray Herbarium of Harvard University, October 2, 1941". There is no archival evidence that Nuttall gifted this or other Gambel collections to John Lowell prior to his return to England, but it is possible that Lowell received specimens directly from Gambel (J. Reveal, Cornell University, personal communication). A specimen at K, labeled as "Sta Fee", Gambel [K 769149], with a stamp indicating "ex Herbarium Hookerianum, 1867", is most likely from the same gathering.

Kearney and Peebles (1943) admitted they had not seen the type, nor could they find one at PH or GH. The image of the designated lectotype at GH has several intact flowers, with calyces estimated to be 4.5–5 mm long, corolla tubes to be 7–9 mm long, rounded to obtuse, elliptic to obovate lobes, and short stamens included in or slightly exserted from the throat. These features are consistent with more recent collections from the Rio Grande Valley in Rio Arriba, Santa Fe, and Taos counties, New Mexico (see Representative Specimens).

Diagnostic description. Flowering stems 10–48 cm, ascending to erect, subglabrous to glandular- and eglandular-puberulent, sometimes sparsely villosulous. Mid-cauline leaves 1–2.2 cm, entire or pinnatifid, the lobes 2–3(5), sparsely glandular and eglandular-puberulent. Inflorescence branches each with 5–14 flowers. Calyx lobe mucros 0.3–1.3 mm. Corolla radial to weakly bilaterally symmetrical, tube and throat lavender to violet, 4–13 mm long; throat 1.5–3 mm wide; lobes pale lavender or violet, sometimes with purple streaks or proximal white patches alternating with purple streaks, equal to subequal in length and width, elliptic, oblong, or obovate, 3–4.5 mm long, 1.5–3 mm wide, apices obtuse, rounded, or truncate, often apiculate. Staminal filaments subequal to unequal, straight to declinate, 0.5–7 mm; anthers strongly exserted; styles 5–14 mm.

Ipomopsis multiflora (Nutt.) V.E.Grant subsp. **multiflora**

Diagnostic description. Calyces (including lobes) 4–6.5 mm; mucros 0.5–0.9 mm long. Corolla radial; tubes 7–10(12) mm long, exserted from calyces; lobes oblong to obovate, lavender to violet, rarely purple, sometimes with proximal purple streaks on 2 or 3 of the lobes, equal to subequal, 4–5 mm long, 1.5–2 mm wide, apices obtuse to rounded. Staminal filaments subequal, 1–5 mm, straight, included in the throat or the longest exserted.

The lectotype at GH and syntype at K are similar, with entire mid-cauline leaves, corolla tubes 7–9.5 mm long, obovate corolla lobes, and stamens located in or at the mouth of the upper corolla throat.

Representative specimens: USA. ARIZONA. **Apache Co**.: Crazy Creek, 19 Sep 1938, *Eastwood and Howell 6899* (CAS); Petrified Forest, 20 Oct 1928, *Eastwood 15737* (CAS); 9 mi S of Springerville, 29 Aug 1946, *Pultz 1906* (CAS, GH); Petrified Forest National Park, Dead Wash, 16 Sep 1992, *Rowlands 92* (ASC); **Graham Co**.: AZ Hwy 366, 6.9 mi SW of the junction with US 161, 4 Aug 2005, *Porter 14492* (BRY); Graham Mtns, 14 Sep 1914, *Thornber* 8025 (ARIZ); Pinaleno Mountains Swift Trail at Wet Canyon Campground, 11 Sep 1976, *Lehto 20587* (ASU); **Greenlee Co**.: just below Sardine Saddle, 24 Jul 1973, *Pinkava 11274* (ASU); 0.5 miles south of Granville Recreation area, 7 Sep 1968, *Lehto 13524* (ASU). COLORADO. **Conejos Co**.: Big Horn Ck, 3.6 mi SW of Canon, 4.1 mi S of Fox Ck, 21 Jul 1986, *Douglas 1266* (CS). NEW MEXICO. **Bernalillo Co**.: near San Antonio, Sandia Mountains, 18 Sep 1932, *Castetter 1359* (RM); NM Hwy 14, 6.2 mi S of US Hwy 66, 24 Aug 1973, *Holmgren and Holmgren 7376* (NMC); **Catron Co**.: Datil Mtns, 10 Aug 1976, *Fletcher 907* (UNM); NM [Highway] 12, NE of Apache Creek, in Tularosa River drainage, 17 Aug 2001, *Hammond 11854* (ASC); 3 mi SW of Mogollon, 27 Aug 1967, *Hess 1431* (NMC); **Cibola Co**.: NM Highway 117, 2 mi S of Villa de Cubero, 25 Aug 1993, *Helmkamp 7-4* (CAS, UCR); El Morro Nat Monument, 3 Sep 2006, *Rink s.n.* (ASC, UNM); East of Ramah, 26 Jul 1906, *Wooton s.n.* (NMC); **Grant Co**.: Mule Creek, 3 Sep 1961, *Osborn 990* (UNM); Mangas Springs, 18 mi NW of Silver City, 5 Sep 1903, *Metcalfe s.n.* (NMC); **McKinley Co**.: NE of Ramah, 6 Aug 1954, *Castetter 9988* (UNM); South of Todilto Park area, 1.25 mi northeast of Twin Hills, Navajo Nation, 13 Sep 2000, *Clifford 771* (NAVA, UNM); **Rio Arriba Co**.: 3 mi S of the old Largo School, Gonzalez Mesa, 6 Aug 1995, *Heil 9367* (UNM); ca. 8 miles north of Gobernador, 22 Aug 1991, Heil s.n. (UNM); **Sandoval Co**.: near Cuchil Arroyo, *Reveal 960* (SBBG); Kasha-Katuwe Tent Rocks National Monument, 21 Sep 2004, *Tonne s.n.* (UNM); **San Juan Co**.: 2 miles northeast of Ozilna Odili east of Highway 544, south of Huerfano Mountain, 3 Aug 2004, *Clifford 30515* (UNM); 6 mi. W of Naschitti, Navajo Nation, 31 Aug 1985, *Ryan 839* (NAVA); **Santa Fe Co**.: roadside near Santa Fe, 1 Oct 1932, Castetter 10010 (UNM); near jct of Hyde Park Rd (Hwy 475) and Gonzalez Rd, E of Santa Fe, 2 Sep 2014, *Wilken and Painter* 17997 (SBBG); Hwy 73 (Tesuque Village Rd) 1.1 mi N of jct with US Hwy 84/285, 29 Aug 2015, Wilken 18007 (ASU, SBBG); **Sierra Co**.: Rastus Flat, Black Range, 12 Aug 1982, *Fletcher 6508* (UNM); Sawmill Peak area, Black Range, 12 Aug 1982, *Hutchins 10235* (UNM); **Socorro Co**.: US 60 opposite turnoff to Mt. Worthington [Withington], 24 Jul 1983, Ertter 4929 (CAS, UC, UCR); Water Canyon, Magdalena Mtns, 14 Sep 1974, *Hutchins* 5268 (UNM). **Taos Co**.: Picuris Indian Pueblo, San Lorenzo, 1 Aug 1961, *Dixon A-222* (UNM); about 4 air mi E of Tres Ritos, Sangre de Cristo Range, 8 Aug 2005, *Larson 3890* (NMC, RM); Cañada Embudo, ca. 10 air mi E of Ojo Caliente, 1 Aug 2006, *Nelson 69308* (RM); **Torrance Co**.:, road to Capilla Peak, 1/2 mile NW of Manzano, Manzano Mountains, 29 Jul 1962, *Bedker 264* (UNM).

Ipomopsis multiflora (Nutt.) V.E.Grant subsp. **brachysiphon** (Wooton & Standley) Wilken, *comb. & stat. nov*. Basionym: *Gilia brachysiphon* Wooton & Standley, Contrib. U. S. National Herbarium 16:160. 1913. *Gilia polyantha* Rydb. var. *brachysiphon* (Wooton & Standley) Kearney and Peebles, Madroño 7:62. Type: USA. New Mexico. Dona Ana Co.: Van Patten's, Organ Mtns, 29 Aug 1894, *Wooton s.n.* (Holotype: US! [US 737120); Isotype: US! [US 561092]).

The types have flowers with calyces 4.5–5 mm long, corolla tubes 5–6 mm long, lobes obovate, their apices rounded, and exserted stamens with filaments 3.5–5 mm long.

Diagnostic description. Calyces (including lobes) 4.5–6 mm; mucros 0.9–1.3 mm long. Corolla radial; tubes 5–8 mm long, included within or slightly exserted from calyces; lobes obovate, lavender to violet, sometimes with proximal purple streaks, equal to subequal, 3–5 mm long, 1–2.5 mm wide, apices rounded. Staminal filaments 3.5–7 mm, straight, exserted.

Representative specimens: NEW MEXICO. **Dona Ana Co**.: Organ Mtns, 4 Sep 1898, *Cockerell s.n.* (NMC); Organ Mountains, 1 Sep 1897, *Wooton 440* (CAS, NMC, RM); Fillmore Canyon, Organ Mtns, 20 Sep 1908, *Wooton and Standley s.n.* (NMC); south side of San Augustin Pass [Organ Mtns], 18 Sep 1999, *Worthington 28680* (UCR, UTEP); San Augustin Pass 0.2 mi SW from crest, 28 Nov 1998, *Worthington s.n.* (SBBG); **Sierra Co**.: south end of the Black Range, Kingston, 29 Aug 1904, *Metcalfe 1269* (CAS, NMC, UNM); east side of Kingston along Percha Creek and Two Springs, Black Range, 31 Aug 1985, *Worthington 13441*, (UCR, UTEP); **Socorro Co**.: South end of the San Mateo Mtns, 28 Aug 1963, *Goodrow 914* (UNM).

Ipomopsis multiflora (Nutt.) V.E.Grant subsp. **whitingii** (Kearney & Peebles) Wilken, *comb. & stat. nov*. Basionym: *Gilia polyantha* Rydb. var. *whitingii* [as *whitingi*] Kearney and Peebles, Madroño 7: 62. 1943. Type: USA. Arizona. Coconino Co.: 2 mi So of Grandview Point, Grand Canyon, South Rim, 13 Aug 1941, *Whiting 1072/5200* (Holotype: US! [US1814983]; Isotypes: ASC! MNA!).

The holotype at US and isotypes at ASC and MNA are consistent with the diagnosis and key in Kearney and Peebles (1943), but also have flowers with long, subequal, declinate stamens, which were not otherwise mentioned in the original description.

Etymology

Kearney and Peebles (1943) did not provide the etymology of var. *whitingii.* Alfred F. Whiting (1912–1978) was a prominent ethnobiologist, associated with the University of Arizona, Dartmouth College, and the Museum of Northern Arizona in Flagstaff (Bartlett 1981). Herbarium specimens of his collections at MNA usually display two numbers, separated by a forward slash (e.g., 1072/5200). The first represents a traditional museum accession or catalog number; the second is equivalent to a unique collection number (Kirstin Phillips, Museum of Northern Arizona, pers. comm.). For example, catalog number 1072 represents a series of collections (5195–5204) made on the south rim of the Grand Canyon near Grand View Point on August 13, 1941.

Diagnostic description. Calyces (including lobes) 4.5–5.5 mm; mucros 0.3–0.7 mm long. Corolla weakly bilaterally symmetrical, usually with 2–3 erect to spreading (adaxial) lobes and 2–3 descending (abaxial) lobes; tubes 6–12 mm long, exserted from calyces; adaxial lobes elliptic to obovate, with purple streaks or proximal white patches alternating with purple streaks, 2.5–5 mm long, 1.5–2.2 mm wide, abaxial lobes elliptic to narrowly elliptic, 3–4.5 mm long, 1.2–2 mm wide, lavender to violet, rarely with proximal marks. Staminal filaments unequal, 3–7.5 mm, exserted, the shortest ones straight, the longest declinate.

Representative specimens: USA. ARIZONA. **Cochise Co.**: Bowie, 16 Sep 1884, *Jones 4239* (ARIZ, CAS); **Coconino Co.**: Walnut Canyon, 29 Sep 1946, *Arnberger 11* (CAS, MNA); Cosnino, 8 Aug 1884, *Jones 4043*, (ARIZ, CAS, RM, RSA); Forest Road 218 on Milk Ranch Point, ca 3.5 air mi NE of Pine, Mogollon Rim, 31 Aug 2006, *Nelson and Fowler 70770* (RM); south of Cosnino, north of the jct of Cosnino Canyon Road and Interstate 40, 24 Aug 2004, *Porter 14180* (ASU); US Hwy 89 between Elden Pueblo and jct of Townsend-Winona Rd and US Hwy 89; 10 Sep 1995, *Wilken 15198* (ASU, SBBG); USFS Rd 237, ca. 0.5 mi E of jct with US89A, W of Pumphouse Wash, 8 Sep 1995, *Wilken 15197* (ASU, SBBG); just E of jct of St Hwy 64 and Garland Prairie Rd, 29 Aug 2014, *Wilken & Painter 17995* (SBBG); **Gila Co.**: Strawberry Hill, Mogollon Rim north of Pine, 10 Sep 1935, *Collom 436* (ASU, RM); Parker Creek Canyon, Sierra Ancha, 12 Aug 1946, *Gould 3660* (ARIZ, CAS, UCR); 12.2 mi SW of Seneca, 19 Aug 1988, *Van Devender et al. 88-456* (ARIZ); Pinal Mountains, south of the town of Globe, 18 Aug 1980, *Forbes 1401* (ASU); SE side of jct of Mogollon Trail (Coconino Forest Rd 319B) and St. Hwy 87, 24 Aug 2015, *Wilken 18002* (ASU, SBBG); **Maricopa Co.**: Cave Creek, 6 Oct 1958, Pase 1021 (ARIZ, RM); Rogers Canyon, ca 1–1.25 mi northwest of Rogers Trough, Superstition Mtns, 29 Sep 1993, *Hodgson 7471* (ASU); **Mohave Co.**: 0.5 mi south of Pigeon Junction, Shivwits Plateau, 28 Jun 1979, *Coombs & Bundy 2877* (ASC); Kanab Plateau, near Tuckett Canyon rim, Grand Canyon Nat Park, 7 Sep, 1953, *Cottam 13893* (CAS, GCNP); Hualapai Mountain State Park, 5 Sep 1987, *Franklin 5216* (RM); Mount Trumbull, 15 Sep 2004, *Higgins 26140* (RM); Cerbat Mountains, 20 Jul 1977, *Jordan* (MNA); **Navajo Co.**: ca 3 mi ESE of Heber, 2 mi NNE of Overgaard, S of Hwy 277, near Apache Lane, 5 Sep 1992, *Ertter 11292* (ASU); Zane Gray Acres, 4 miles northeast of Heber, 12 Oct, 1963, *Lehto 3533* (ASC, ASU); **Pima Co.**: 2 mi above Molino Basin, Santa Catalina Mountains, 1 Oct 1951, *Parker 7698* (ARIZ); Baboquivari Mountains, along jeep trail east of and within 3/4 mile of Thomas Canyon - Max Seep area, 13 Sep 1985, *Hodgson 3937* (UCR); Sabino Canyon, Santa Catalina Mountains, 27 Sep 1934, *Kearney & Peebles 10330* (ARIZ); **Pinal Co.**: Mount Lemmon road from Oracle, between control stations, 2 Sep 1938, *Benson 9100* (ARIZ); Table Mountain, north end of Galiuro Mountains, 27 Aug 1980, *Warren 307* (ARIZ); **Yavapai Co.**: 3.0 km ENE of Inscription Canyon [Williamson Valley], 18 Aug 1990, *Baker 7932* (ASC); South of Prescott, Sep 1950, *Blakley 919* (DES); 6 miles W of Cleator along road to Crown King, Bradshaw Mtns, 18 Aug 1974, *Gentry 23424*, (DES image); Sterling Canyon, W of Oak Creek Canyon, 24 Aug 2004, *Hartman 80392* (RM); ca 10 mi southeast of Prescott, 14 Sep 1987, *Landrum 5608* (ASU); Anvil Rock Rd, 12 mi W of Seeligman, 27 Sep 1997, *White 5704* (ASU, RSA, UCR). NEW MEXICO. **Cibola Co.**: El Calderon, El Malpais Nat Monument, 3 Oct 2005, *Chauvin* (UNM); **Grant Co.**: Cane Spring Canyon, Bear Mtn, 11 Sep 1980, *Fletcher 4929* (UNM); N of Central, 5 Sep 1941, *Clark 10593* (UNM); **McKinley Co.**: Navajo Experiment Station, 18 Sep 1938, *Eastwood 6864* (CAS).

Intermediate populations. Some specimens from Apache and Navajo counties, Arizona and Catron, Cibola, and McKinley counties, New Mexico have flowers with subequal, obovate corolla lobes but with the longest stamens slightly curved. Other specimens from the same general area have straight, subequal filaments up to 7 mm long. The co-occurrence of subsp. *multiflora* and *whitingii* in western New Mexico and eastern Arizona suggests either hybridization or the existence of uniform populations representing primary intergradation. A few enigmatic specimens possessed radial corollas with narrowly oblong corolla lobes and straight, exserted stamens. Future studies need to include *in situ* observation and photographic documentation of corolla symmetry and lobe coloration to clarify variation within the species. A cladistic analysis using molecular methods from throughout the range of distribution is highly desirable.

Representative specimens: USA. ARIZONA. **Apache Co.**: Window Rock, Navajo Nation, 19 Aug 1961, *Bohrer 650* (NAVA); **Navajo Co.**: ca. 3 mi ESE of Heber, 5 Sep 1992, *Ertter 11292* (ASU). NEW MEXICO. **Catron Co.**: Datil Mountains, 10

Aug 1976, *Fletcher 907* (UNM); NE of Apache Creek, 17 Aug 2001, *Hammond 11854* (ASC); **Cibola Co.**: 2 mi E of Cibola Canyon Campground, 15 Aug 1961, *Osborn 888* (UNM); El Morro National Monument, 3 Sep 2006, *Rink 5220* (ASC, UNM); **McKinley Co.**: 4 miles south of Fort Wingate, 25 Aug 1993, *Helmkamp 5-4*, (UCR); canyon above Red Rock State Park, 12 Sep 1997, *Sivinski 4135* (UNM); Interstate 40, 30 mi east of Gallup at Coolidge (exit 44), 8 Aug 1987, *Sanders 7191* (UCR).

Diagnostic Key

1. Corolla radial, lobes widely elliptic to ovate, white or faintly bluish, with pink to violet flecks; mid-cauline leaves 2–3.3 cm, pinnatifid, the lobes 3–5; calyx lobe mucros 0.1–0.5 mm . . . . *Ipomopsis polyantha*

1′ Corolla radial or weakly bilaterally symmetrical, lobes elliptic, oblong, or obovate, pale lavender or violet, not flecked, sometimes with purple streaks and proximal white patches alternating with purple streaks; mid-cauline leaves 1–2.2 cm, entire or pinnatifid, the lobes 2–3(5); calyx lobe mucros 0.3–1.3 mm . . . . *Ipomopsis multiflora*

2. Corolla weakly bilateral, usually with 2–3 erect to spreading (adaxial) lobes and 2–3 descending (abaxial) lobes, the adaxial lobes with proximal purple streaks or white patches alternating with purple streaks; stamens unequal, the shortest ones straight, the longest declinate . . . . *Ipomopsis multiflora* subsp. *whitingii*

2′ Corolla radial, lobes lavender to violet, sometimes flecked or proximally streaked; stamens equal to subequal, straight, not declinate

3. Corolla tubes 5–8 mm long, included within or slightly exserted from the calyces; stamens 3.5–7 mm long, all exserted . . . . *Ipomopsis multiflora* subsp. *brachysiphon*

3′ Corolla tubes 7–10 mm long, exserted from the calyces; stamens 1–4 mm long, included in the throat or the longest exserted . . . . *Ipomopsis multiflora* subsp. *multiflora*

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NOMENCLATURAL CHANGES IN *CYLINDROPUNTIA* (CACTACEAE)

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ABSTRACT

The following nomenclatural novelties are established in the genus *Cylindropuntia*: *C. acanthocarpa* subsp. *ramosa* (Peebles) M.A.Baker & Cloud-H., *C. alcahes* subsp. *gigantensis* (Rebman) Rebman; *C. alcahes* subsp. *mcgillii* (Rebman) Rebman; *C. ganderi* subsp. *catavinensis* (Rebman) Rebman; *C. imbricata* subsp. *rosea* (DC.) M.A.Baker; *C. imbricata* subsp. *spinosior* (Engelmann) M.A.Baker, Cloud-H. & Majure; *C. imbricata* subsp. *spinotecta* (Griffiths) M.A.Baker; *C. thurberi* subsp. *versicolor* (Engelmann ex J.M.Coulter) M.A.Baker; *C. whipplei* subsp. *enodis* (Peebles) M.A.Baker. A lectotype is designated for the name *Opuntia whipplei* var. *enodis* Peebles.

Key Words: *Cylindropuntia*; DNA analysis; geography; lectotypification; morphology; nomenclatural changes; ploidy.

This paper proposes a number of nomenclatural changes, along with relevant synonymies, within the genus *Cylindropuntia* (Engelmann) F.M.Knuth. Many of the taxa treated here were previously placed in the genus *Opuntia* and later transferred to *Cylindropuntia* (Knuth 1930; Backeberg and Knuth 1935; Backeberg 1958; Pinkava et al. 2001). Turner and Nesom (2000) present a reasonable argument for using varieties as a primary taxonomic unit below the species level. They quote the Saint Louis Code (Greuter et al. 2000), which in Art. 4.1 lists variety as the only secondary rank between species and form and states that, if additional ranks are needed, then subspecies may be used between species and variety (Art. 4.2). However, the newest code (Turland et al. 2018) includes a note after Art. 4.2 that the rank subspecies may be used whether or not a variety rank has been adopted. A thorough presentation of the historical uses of varieties and subspecies is given by Clausen (1941), who, while not disregarding the need for the rank of variety, argues that subspecies should be used when ample empirical data are available and/or there exists a well-established geographic and/or ecological distribution that mostly differs from other subspecies. Stebbins (1950) had a similar concept, stating:

> The subspecies or geographic variety is a series of populations having certain morphological and physiological characteristics in common, inhabiting a geographic subdivision of the range of the species, or a series of similar ecological habitats, and differing in several characters from typical members of other subspecies, although connected with one or more of them by a series of intergrading forms.
>
> (p. 33)

Pederson (1998) presents a similar view to that of Clausen and Stebbins and suggests that autotetraploids should be treated as conspecific with their diploid progenitors. Although cactus taxonomists have recently used subspecies to circumscribe populations that are geographically correlated with morphology (Baker 2006; Baker and Butterworth 2013; Baker and Porter 2016; Majure et al. 2017), some authors have made subspecies designations with little or no associated empirical or geographical data.

The following new combinations are made after many years of cytological, morphological, DNA, common garden, and herbarium studies by the authors and their colleagues, which have shown that certain groups of *Cylindropuntia* populations possess a unique combination of morphology, ploidy, and distribution, but cannot be easily separated by DNA sequencing from a sister taxon or sister taxa. In addition, all of our subspecies occur within a fairly unique distribution, but morphologically intergrade with a sister taxon or sister taxa where their distributions overlap.

NOMENCLATURE

Cylindropuntia acanthocarpa subsp. **ramosa** (Peebles) M.A.Baker & Cloud-H. stat. nov. *Opuntia acanthocarpa* Engelmann & J.M.Bigelow var. *ramosa* Peebles, Cact. Succ. J. (Los Angeles) 9:37. 1937. *Cylindropuntia acanthocarpa* var. *ramosa* (Peebles) Backeberg, Cactaceae (Backeberg) 1:181. 1958. Lectotype: USA, Arizona, Pinal County, near Sacaton, cultivated, 1920, *A. R. Leding SF* 2. (US 1699996!) The type sheet has specimens collected on more than one date and thus represents multiple gatherings: Mounted stem with single dry flower was designated as the lectotype by M Baker (Baker et al. 2018), Isolectotype: stems with flowers (ARIZ 94443!).

Populations of this subspecies occur in the eastern Sonoran Desert, as opposed to the typical subspecies, which occurs primarily in the western Sonoran and Mojave deserts. The third subspecies, *C. acanthocarpa* subsp. *thornberi* (Thornber & Bonker) Lodé occurs in the highlands of central Arizona. A statistical correlation among the geographical range and morphology of the subspecies (as varieties) was reported by Baker et al. (2018), and a DNA study of the diploid species within the genus supports these taxa as belonging to a singles species (Majure et al. *in review*).

Cylindropuntia alcahes subsp. **gigantensis** (Rebman) Rebman stat. nov. *Cylindropuntia alcahes* var. *gigantensis* Rebman, Madroño 62(1):47, fig. 1, map 2. 2015. Holotype: MEXICO, Baja California Sur, 111°58′W, 26°19′N, lava fields on the road to La Purísima, 24 May 1992, *Rebman et al. 1404*, ASU 187536!; Isotypes: BCMEX 5106, HCIB 3277; DES 00037111!.

Cylindropuntia alcahes subsp. *gigantensis* (Rebman) U.Guzmán, Cactaceae Syst. Init. 16:16. 2003, nom. inval. (based on an unpublished basionym).

Endemic to Baja California Sur, from the Sierra El Giganta, north to the Sierra El Mezquital (Rebman 2015).

Cylindropuntia alcahes subsp. **mcgillii** (Rebman) Rebman stat. nov. *Cylindropuntia alcahes* var. *mcgillii* Rebman Madroño 62(1):50, figs. 2 (map), 3. 2015. Holotype: MEXICO, Baja California, 115°47′W, 30°09′N, ca. 8 mi N of El Rosario along Rte. 1 at km marker 42, 31 May 1991, *Rebman 1219* & *Cota*, ASU 186273!; Isotypes: BCMEX 5581, SD 137583.

Cylindropuntia alcahes subsp. *mcgillii* (Rebman) U.Guzmán, Cactaceae Syst. Init. 16:16. 2003, nom. inval. (based on an unpublished basionym).

The subspecies is restricted to approximately 200 km of coastal scrub near El Rosario, Baja California (Rebman 2015).

Cylindropuntia ganderi (C.B.Wolf) Rebman & Pinkava subsp. **catavinensis** (Rebman) Rebman stat. nov. *Cylindropuntia ganderi* (C.B.Wolf) Rebman & Pinkava var. *catavinensis* Rebman, Madroño 62(1):55. 2015, Holotype: MEXICO, Baja California, 114°46′W, 29°47′N, Rte. 1, ca. 2 mi N of Cataviña and 3 mi S of the road to San José Faro, 23 Apr 1993, *Rebman 1723* & *Davis*, ASU 190076!, Isotypes: BCMEX 5854, SD 136474!.

Cylindropuntia ganderi subsp. *catavinensis* (Rebman) U.Guzmán, Cactaceae Syst. Init. 16:16. 2003, nom. inval. (based on an unpublished basionym)

The subspecies is restricted to about 100 km north to south, in the vicinity of Cataviña, Baja California, while the typical subspecies occurs in the northern Sierra San Pedro Mártir, Baja California to southern California, in the western Sonoran Desert (Rebman 2015).

Cylindropuntia imbricata (Haworth) F.M.Knuth subsp. **rosea** (DC.) M.A.Baker. stat. nov. *Opuntia rosea* DC. Prodr. (A.P.deCandolle) 3:471. 1828. *Cylindropuntia rosea* (DC.) Backeberg Cactaceae (Backeberg) 1:197. 1958. *Cylindropuntia imbricata* (Haworth) F.M.Knuth var. *rosea* (DC.) M.A.Baker Haseltonia 25:13. 2018. Holotype: figure of *Cactus quadrifolius* in Mociño, Fl. Mex. ined., DC. no. 406, preserved in the Hunt Institution for Botanical Documentation no. 880.

This subspecies represents the southern geographical morphotype of the species occurring in the San Luis Potosí/ Guanajuato desert grasslands and distinguished by greener stems, fewer spines, less tuberculate fruits, and smaller, paler flowers than those of the typical subspecies (Baker and Pinkava 2018).

Cylindropuntia imbricata (Haworth) F.M.Knuth subsp. **spinosior** (Engelmann) M.A.Baker, Cloud-H. & Majure stat. nov. *Opuntia whipplei* Engelmann & J.M.Bigelow var. *spinosior* Engelmann, Proc. Amer. Acad. Arts 3: 07. 1856. Opuntia spinosior (Engelmann) Toumey Bot. Gaz. 25: 119. 1898. *Cylindropuntia spinosior* (Engelmann) F.M.Knuth, Kaktus-ABC [Backeberg & Knuth] 126. 1936. *Cylindropuntia imbricata* (Haworth) F.M.Knuth var. *spinosior* M.A.Baker, Cloud-H. & Majure, Haseltonia 25:13. 2018. *Grusonia spinosior* (Engelmann) Goodwyn ex G.D.Rowley, *Tephrocactus* Study Group 12(3):45. 2006. Lectotype: Designated by L. D. Benson (Benson 1982), *Schott, no. 5*, June 1855, MO 2015359!, Isolectotype: POM 317797!.

Opuntia spinosior var. *neomexicana* Toumey, Bot. Gaz. 25:119. 1898.

This subspecies represents Sonoran Desert populations of the species and is differentiated from other

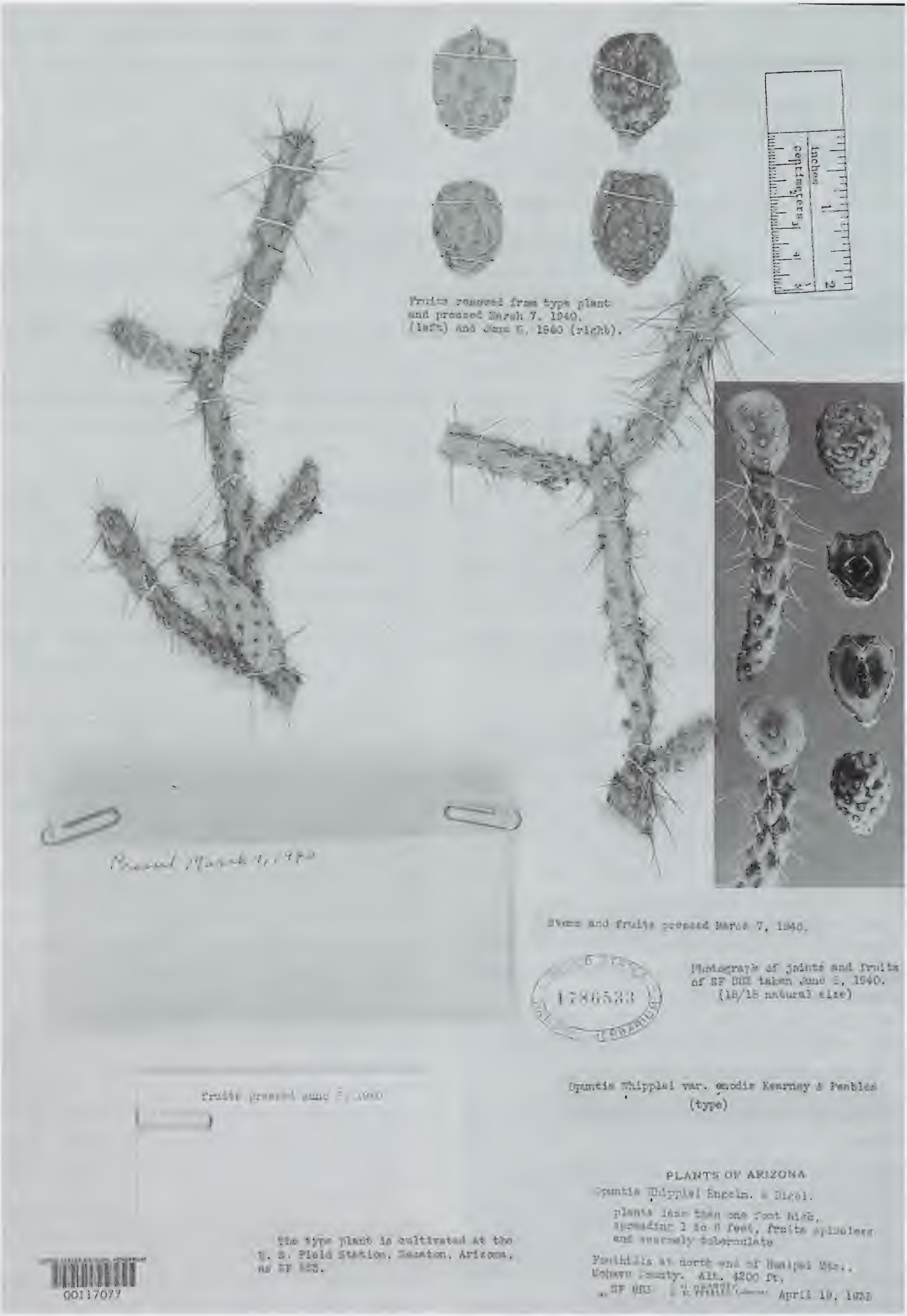
Fruits removed from type plant
and pressed March 7, 1940,
(left) and June 6, 1940 (right).
inches
centimeters
Pressed March 7, 1940
Stems and fruits pressed March 7, 1940.
1786533
Photograph of joints and fruits
of SF 883 taken June 6, 1940.
(15/18 natural size)
fruits pressed June 6, 1940
Opuntia Whipplei var. enodis Kearney & Peebles
(type)
PLANTS OF ARIZONA
Opuntia Whipplei Engelm. & Bigel.
Foothills at north end of Hualpai Mts.,
Mohave County. Alt. 4200 ft.
SF 883
April 19, 1935
The type plant is cultivated at the
U. S. Field Station, Sacaton, Arizona,
as SF 883.
00117077

FIG. 1. Type sheet of *Opuntia whipplei* var. *enodis*, *Peebles SF 883*, US 1786533. LECTOTYPE: The two fruits in the upper right-hand corner of the sheet labeled "Fruits removed from type plant… and pressed June 6, 1940 (right)", contents of packet on the lower left-hand corner of the sheet labeled "fruits pressed June 6, 1940"; and photograph labeled "Photograph of joints and fruits of SF883 taken June 6, 1940 (15/18 natural size)".

subspecies by shorter spines and lower, more crowded tubercles. The placement of *Cylindropuntia spinosior* within *C. imbricata* resulted, in part, from recent DNA analyses (Baker and Pinkava 2018, Majure et al. *in review*)

Cylindropuntia imbricata subsp. **spinotecta** (Giffiths) M.A.Baker stat. nov. *Opuntia spinotecta* Griffiths, Proc Biol. Soc. Wash. 27:24. 1914. *Cylindropuntia imbricata* var. *spinitecta* (Giffiths) M.A.Baker Haseltonia 15:119. 2009. Holotype: MEXICO, Durango, 28 September 1909, *Griffiths 9859*, US 3053030, Isotype: POM288220!.

This subspecies represents populations of the species occurring in the highlands of Durango and Zacatecas, distinguished from the typical subspecies by fewer central spines per areole, lower and narrower stem tubercles, and the presence of at least some fusiform, tuber-like roots (Baker et al. 2009).

Cylindropuntia thurberi (Engelmann) F.M.Knuth subsp. **versicolor** (Engelmann ex J.M.Coulter) M.A.Baker comb. & stat. nov. *Opuntia versicolor* Engelmann ex J.M.Coulter, Contr. U.S. Natl. Herb. 3(7):452. 1896. *Opuntia thurberi* subsp. *versicolor* (Engelmann ex J.M.Coulter) Felger, J. Arizona Acad. Sci. 6:83. 1970. *Cylindropuntia versicolor* (Engelmann ex J.M.Coulter) F.M.Knuth Kaktus-ABC [Backeb. & Knuth] 125. 1936. Lectotype: Designated by L. D. Benson (Benson 1982), Mesas and foothills, 18 May 1881, *C. G. Pringle s. n.*, MO 2015376!, Isolectotypes: AC 00320516!; CM 284297!; F 98068!, 404515; G 00236625!, 00236570!; GH 00063179!; ISC 249224!; K 000100821!; MO 2015374!; NY 00386010!; P 4515904!; PH 01077601!; RSA 313597!; US 41045, 795896; VT 024793!.

Opuntia versicolor Engelmann ex Toumey, Gard. & Forest 8 (no. 390): 325, adnot., 326. 1895; nom. inval. (without description).

This subspecies represents populations of the species occurring in the Sonoran Desert and having thicker stems, shorter tubercles and longer, more numerous spines than the typical subspecies. Although the typical subspecies is often considered to occur primarily in the subtropical deciduous forest (Sonoran-Sinaloan transition subtropical dry forest), it also occurs in upland habitats of the Sierra Madre Occidentale (see Felger and Lowe 1970), which includes the type locality for the species

Cylindropuntia whipplei (Engelmann & J.M.Bigelow) F.M.Knuth subsp. **enodis** (Peebles) M.A.Baker stat. nov. *Opuntia whipplei* Engelmann & J.M.Bigelow var. *enodis* Peebles, J. Wash. Acad. Sci. 30:473. 1940, Cylindropuntia whipplei var. enodis (Peebles) Backeb. Cactaceae (Backeberg) 1:180. 1958. Type: USA, Arizona, Mohave Co., "North end of Hualapai Mountain, Mohave County, Ariz., altitude 4200 ft, *Peebles SF 883*, April 19, 1935," referring to a plant collected from the field on that day and then cultivated at the U. S. Field Station, Sacaton, Arizona. Apparently, no material was processed as an herbarium specimen at that time. Type Sheet: US 1786533!. The sheet, which has the word "type" in the same typewritten font as the main label, has materials collected on more than one date and thus represents multiple gatherings (see Art 8.2 Turland et al. 2018), Lectotype: Designated here by M. A. Baker as material collected June 6, 1940 on US 1786533 (Fig. 1): The two fruits in the upper right-hand corner of the sheet labelled "Fruits removed from type plant... and pressed June 6, 1940 (right)", contents of packet on the lower left-hand corner of the sheet labelled "fruits pressed June 6, 1940"; and photograph labelled "Photograph of joints and fruits of SF883 taken June 6, 1940 (15/18 natural size)". Isolectotypes: ARIZ 95988! (the word "isotype" is handwritten on the sheet), CAS 548490! (the word "isotype" is typed on the label).

Although Peebles specifies April 19, 1935 as the date of collection, this referred only to the living material that was planted at the U. S. Field Station, Sacaton, Arizona, under the living collections number SF883. The herbarium material collected June 6, 1940 was obviously seen by him before he submitted his and Wheeler's manuscript, which was received by the publisher August 6, 1940. Unfortunately, the material labelled May 7, 1940 on the US sheet, is more complete, comprising both stems and fruits. The June 6, 1940 material is selected as the lectotype because it is the same date that the materials were collected for CAS and ARIZ isolectotypes. In Peebles' protologue, he mentions only that the fruit tubercles of *O. whipplei* var. *enodis* are "broad, low, and not prominent" in comparison to the typical variety, thus the presence of fruits and a photograph of the fruits on the lectotype is sufficient to represent the taxon. Note that there was no other material mentioned in the protologue beyond SF883 and no indication that any material was collected as an herbarium specimen on the date that the live material was collected from the field.

This subspecies represents tetraploid populations of the species occurring primarily in the Mojave Desert and having a more diminutive habit, smaller stems, fewer spines, and less tuberculate fruits than the typical diploid subspecies. Morphological differences between the two subspecies are less pronounced at higher elevations where the two subspecies are sympatric (Baker 2016).

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NOTES ON *LYTHRUM* (LYTHRACEAE) IN CALIFORNIA: *LYTHRUM JUNCEUM* AS A NEW (BUT OLD) INTRODUCED SPECIES, TYPIFICATION OF GREENE'S *LYTHRUM* TYPES, AND POSSIBLE HYBRIDIZATION OF *LYTHRUM* IN CALIFORNIA

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ABSTRACT

The Mediterranean species *Lythrum junceum* Banks & Sol. is newly reported from California, based on multiple records from southwestern Alameda County and adjacent Santa Clara County. Previous collections, dating to at least 1905, were misidentified as *L. californicum* Torr. & A.Gray, but differ in their sprawling habit, white-based petals, and purple-spotted hypanthia. Diagnostic features, invasive potential, and speculations on origin are addressed. In addition, two species of *Lythrum* described from California in 1889 are typified: a lectotype for *L. adsurgens* Greene and a neotype for *L. sanfordii* Greene. The possible role of hybridization in the establishment of *L. hyssopifolia* L. and other introduced species of *Lythrum* in California is also discussed.

Key Words: hybridization, invasive species, *Lythrum junceum, Lythrum hyssopifolia, Lythrum californicum, Lythrum adsurgens* lectotype, *Lythrum sanfordii* neotype, tristyly.

LYTHRUM JUNCEUM IN CALIFORNIA

Five species of the genus *Lythrum* (Lythraceae) are currently recognized in the California flora: one native (*L. californicum* Torr. & A.Gray) and four non-native (*L. hyssopifolia* L., *L. portula* (L.) D.A.Webb [previously *Peplis portula* L.], *L. salicaria* L., and *L. tribracteatum* Spreng.). Of these, *Lythrum salicaria* is distinctive in its large size and dense spike of showy flowers, while *L. portula* and *L. tribracteatum* are relatively inconspicuous, seldom-encountered plants. The remaining two species, *L. californicum* and *L. hyssopifolia,* are relatively common and widespread in wet habitats throughout most of California (Consortium of California Herbaria 2019). Among other differences, *L. californicum* is generally erect and distally branched with relatively narrow leaves, large short-pediceled flowers, and epicalyx bractlets that are about as long as the sepals, while *L. hyssopifolia* is generally prostrate and proximally branched, with broader leaves, smaller subsessile flowers, and epicalyx bractlets about twice as long as the sepals.

While exploring the recently opened Vargas Plateau Regional Park in southwestern Alameda County, California, in December 2017, the authors encountered a *Lythrum* that seemed to combine features of *L. californicum* (large showy flowers) and *L. hyssopifolia* (sprawling habit and leaf shape). The plants formed a tangled mass of dried stems and inflorescences, dominating a spring area protected from grazing near the main trailhead. After looking at specimens at the University and Jepson Herbaria at UC Berkeley (UC/JEPS) and using the key in *Flora Europaea* (Webb 1968), we identified the plants as *L. junceum* Banks & Sol., subsequently confirmed by Shirley Graham (Missouri Botanical Garden, personal communication), author of Lythraceae for *The Jepson Manual* (Baldwin et al. 2012) and a pending volume of *Flora of North America North of Mexico*.

On a hunch, we then examined two earlier collections by one of us from nearby sites: *Ertter 11558* from Mission Peak in 1993, and *Ertter 14540* from Cushing Drive in 1995. Both had been shoehorned into *L. californicum* on the basis of flower size and epicalyx/sepal proportions, but proved instead to be *L. junceum*. Further sleuthing located several other historical collections of *L. junceum* that had been misidentified as *L. californicum*, all from southwestern Alameda County and adjacent Santa Clara County. The full list of currently known herbarium collections of *L. junceum* from California is presented here:

LYTHRUM JUNCEUM Banks & Sol. (LYTHRACEAE).—Alameda Co., Warm Springs, 28 June 1916, *Abrams 5681* (DS, RSA); Mission Peak Regional Preserve SE of Fremont, steep SW-facing slope above S tributary of Agua Caliente Creek at S edge of preserve, 24 April 1993, *Ertter 11558* (UC); Cushing Road, field northwest of junction with North Port Loop East, 3 November 1995, *Ertter 14540* (RSA, UC, UCR); Vargas Plateau Regional Park, edge of spring-fed wetland near staging area on

Morrison Canyon Road, 10 December 2017, *Ertter & Gowen 22978* (UC, MO), *Gowen 1442* (JEPS), 4 May 2018, *Gowen 1451* (JEPS); SE corner of Mission Peak Regional Preserve, wet ground at edge of stringer and well-grazed spring S of Horse Heaven trail, 27 January 2018, *Ertter et al. 22979* (UC); around pond N of dirt road to Mission Peak, 7 May 2018, *Gowen 1452* (JEPS); N edge of Mission Peak Regional Preserve, 7 May 2018, *Gowen 1453* (JEPS). Santa Clara Co.: Milpitas, April 1905 *Smith s.n.* (DS); in mud of drainage ditch about two miles north of Milpitas, 6 June 1955, *Sharsmith 6272* (SJSU); wet ground along margin of Calaveras Reservoir, about seven miles east of Milpitas, 30 May 1958, *Hillegus 112* (SJSU).

In addition to herbarium specimens, photo-documentation supplements the presence of *L. junceum* in the same areas. Images labeled *L. californicum* in CalPhotos taken by Ron Wolf at Don Edwards National Wildlife Refuge (ID: 0907 0028 & 0907 0029) are clearly *L. junceum,* as is a photo taken by Christopher Thayer near either the Vargas Plateau or Calaveras Reservoir (H. Bartosh, Nomad Ecology, personal communication).

The earliest known collection of *L. junceum* from California is the one from Milpitas in 1905, indicating that the species has been present in California for nearly 115 years. It is now well established in at least southwestern Alameda County, where it is locally dominant in wetland situations. In spite of the length of time and local abundance, the species has not previously been reported from California, and the only other report from North America was as an apparent waif in Massachusetts in 1883 (Cullina et al. 2011).

Lythrum junceum is native to southwestern Europe and the Mediterranean region of southern Europe, the Near East, northern Africa, and Macaronesia (Webb 1968). It has also been introduced to Australia and New Zealand. The species has alternatively been known as *L. acutangulum* Lag. (misapplied), *L. flexuosum* Lag. (misapplied), *L. graefferi* Ten., and *L. meonanthum* Link ex Steudal. We recommend rose loosestrife as a common name, as currently used in New England and New Zealand; alternatives include false grass-poly (Wikipedia, International Union for the Conservation of Nature [IUCN]), Mediterranean loosestrife (Australia), and creeping loosestrife (Malta).

Diagnostic Features of *Lythrum junceum*

In California, *Lythrum junceum* has routinely been misidentified as *L. californicum.* Both of these species are rhizomatous or stoloniferous perennials with relatively large showy flowers, but *L. junceum* is a low matting or mounding plant (Fig. 1A), whereas *L. californicum* is taller and more upright. The petals of *L. junceum* also tend to be white at the base (Fig. 1B), while those of *L. californicum* are not. Notably, the hypanthium of *L. junceum* generally has some red spots near the base (Fig. 1B), which help distinguish it from all other species of *Lythrum* (Webb 1968). In addition, the seeds of the two species differ in shape and texture (Table 1). The seeds of *L. junceum* are roundish and usually have trichomes, while *L. californicum* has seeds which are narrowly teardrop-shaped and merely slightly sculptured.

Thus far, no California collections of *L. junceum* have been located as misidentified *L. hyssopifolia,* though several such sheets were located in the European and African collections at UC. When in flower, the two are easily distinguished, but vegetative characteristics are more overlapping. *Lythrum hyssopifolia* is primarily an annual, at least in Europe, but often persists as a short-lived perennial in California.

The primary characters that serve to distinguish *L. junceum* from *L. californicum* and *L. hyssopifolia,* the two other species occurring in California that are most likely to be confused with *L. junceum,* are summarized in Table 1. Some measurements for *L. californicum* are modified from *The Jepson Manual* (Baldwin et al. 2012), to account for specimens of *L. junceum* that had previously been included in this species.

Invasive Status of *Lythrum junceum*

In addition to conducting herbarium and literature reviews, we returned to several previously documented localities to determine the current status of *Lythrum junceum* in California. Although no plants were located in our single mid-winter visit to Don Edwards San Francisco Bay National Wildlife Refuge, populations were located at almost every wetland site in Mission Peak Regional Preserve, and the species is often a dominant species at these sites. Grazing removes the tangled inflorescences (Fig. 1C) that were prominent in ungrazed sites (as at the spring near the Vargas Plateau trailhead), but the plants themselves continue to thrive vegetatively, spreading by strongly rooted stolons (Fig. 1D). Based on these field observations in 2017 and 2018, we conclude that *L. junceum* can be a serious wetland invader.

Given its invasive potential, the length of time that *L. junceum* has been present in California, and how readily other invasive wetland species are distributed by the movement of cattle, waterfowl, or machinery, it is rather puzzling that *L. junceum* is not more widespread. One possible limiting factor is that the species is self-incompatible due to tristyly, in which outcrossing is promoted by means of three morphotypes that differ in style length and stamen length (Dulberger 1970, Ornduff 1975). Only the long- and mid-styled morphotypes have thus far been found in California, though the absence of the short-styled morphotype is unlikely to significantly reduce sexual reproduction (Dulberger 1970). On the other hand, if

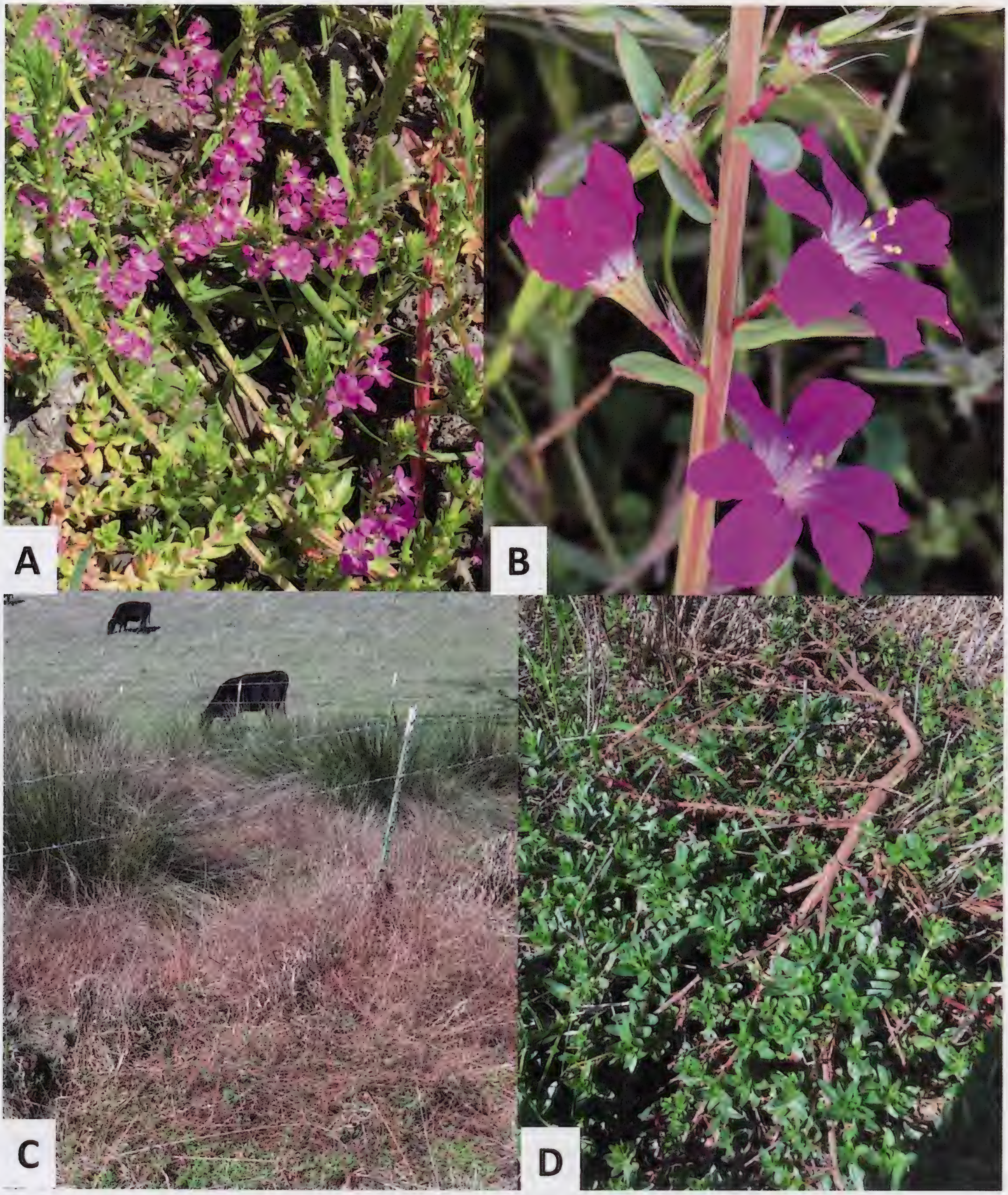

FIG. 1. Habit and flowers of *Lythrum junceum*. A. Sprawling plant in peak bloom. B. Close-up of flowers, showing white petals bases and purple spots on hypanthium. C. Mid-winter habit of tangled reddish brown dried inflorescences along ungrazed fenceline. D. Mid-winter habit of prostrate new growth in a grazed wetland. Photo credit:All photos by David Gowen.

only an individual seed or rooted fragment makes it to a new location, tristylous self-incompatibility would interfere with sexual reproduction if no other morphotype is present.

On the other hand, the species might actually be more widespread than currently realized, with occurrences dismissed as either sprawling *L. californicum* (if flowering) or exceptionally robust *L. hyssopifolia* (if vegetative). The present paper is intended to alert other botanists to this overlooked species, with Table 1 and Fig. 1 provided to assist with identification.

TABLE 1. SUMMARY OF CHARACTERS THAT DISTINGUISH SPECIES OF *LYTHRUM* IN CALIFORNIA THAT ARE MOST LIKELY TO BE CONFUSED WITH *L. JUNCEUM*. Some measurements for *L. californicum* are modified from *The Jepson Manual* (Baldwin et al. 2012), to account for specimens of *L. junceum* that had previously been included in this species.

	L. junceum	*L. californicum*	*L. hyssopifolia*
habit	sprawling, mounding, or matted perennial	erect perennial	erect to spreading annual (or short-lived perennial)
leaf shape	broadly elliptic-oblong, with truncate - almost auriculate base	narrow with tapering base	elliptic-oblong to narrow with truncate - almost auriculate base
pedicel	short	short	absent
hypanthium	obconic with red spots near base	cylindrical, lacking red spots	obconic to cylindrical, lacking red spots
epicalyx bractlets	slightly longer or more prominent than sepals	slightly longer or shorter than sepals	much longer than sepals
petals	5–9 mm long, rose with white base	4–6 mm long, purple throughout	1–3 mm long, pink throughout
stamens	12	6	4–6
styly	tristylous: 2 levels of stamens, style at 3rd level	distylous: stamens at one position, style at other	homostylous: style generally longer than stamens
seeds	+/− ovoid, with trichomes	narrowly lanceoloid, with faint bumps but no trichomes	+/− ovoid, sometimes with trichomes

Speculations on Origin

Although there is no way to determine the timing or the source of the introduction of *Lythrum junceum* with certainty, the proximity of known populations within an eight-mile radius of Mission San José raises some intriguing possibilities. This mission, southeast of the present city of Fremont, was founded in 1797 and was completed by about 1808 (Country Club 1904). The California missions functioned as early centers of population growth and commercial trade, which in turn contributed to the introduction of non-native species (summarized in Bossard and Randall 2007). The agricultural production of Mission San José increased during the decades following establishment, and, by 1834, "24,000 cattle, thousands and thousands of uncounted horses and mules, and 1,900 sheep, goats and hogs" (Country Club 1904) roamed at large throughout the hills near the mission, including both present-day Mission Peak Regional Preserve and Vargas Plateau Regional Park.

Viticulture also became a major agricultural presence in the region following secularization of the missions in 1833 (Holmes and Schaffarcyzk 2013). Much of the stock for these vines was imported from those parts of Europe where *L. junceum* grows; e.g., 10,000 grape cuttings were imported from France and Spain in 1862 (Country Club 1904). One former vineyard, along with a hotel complex called Warm Springs Resort for the springs it was built around, overlaps the base of Mission Peak Regional Preserve where populations of *L. junceum* occur.

Lythrum junceum has also been collected farther downstream at the mouth of Agua Caliente Creek, where Warm Springs landing was established to facilitate the flow of goods and people to San Francisco, and ultimately beyond. When the Western Pacific Railroad line was built through the area in 1866, the station was given the name of Warm Springs (Country Club 1904) and since that time the area has been called the Warm Springs District. Both the landing and the railroad line represent alternate possible vectors for the introduction of non-native species.

Another potential origin for *L. junceum* in California was through the horticultural trade. Beginning in 1868, a large nursery business developed in Niles, a few miles north of Mission San José. It became the California Nursery Company in 1884, and by 1904 was apparently the largest nursery on the Pacific Coast (Country Club 1904). Mack (1991) lists at least 139 alien species that might have been spread throughout the United States as a result of the seed trade, including the noxious weed *L. salicaria*. *Lythrum junceum* is seldom cultivated, but it is listed in *Hortus Third* (Bailey and Bailey 1976), as *L. flexuosum* (misapplied). The large, bright pink flowers (Fig. 1) make *L. junceum* one of the more attractive members of the genus, and immigrants from its native range could have intentionally brought some plants with them as an easily grown reminder of home.

TYPIFICATIONS OF GREENE'S "THE GENUS *LYTHRUM* IN CALIFORNIA"

Our search for early records of *Lythrum junceum* in California led us to Greene's (1889) overview of *Lythrum* in California, in which he recognized four species in the state. In addition to *L. californicum* and *L. hyssopifolia,* he described two new species: *L. adsurgens* Greene and *L. sanfordii* Greene. Greene compared the former to *L. hyssopifolia,* with *L. adsurgens* differing in having even smaller flowers, perennial roots, a stoloniferous crown, and nearly prostrate stems. Whereas he knew of *L. hyssopifolia*, referred to as a "small, homely and obscurely lurking annual," from only two collections in Napa and Sonoma counties, *L. adsurgens* was "plentiful" adjacent to salt marshes in the San Francisco Bay. Although the habit strongly suggests *L. junceum*, the small flowers prevent *L. adsurgens* from being this species.

Greene's other new species, *Lythrum sanfordii*, was distinguished from the other three species on the basis of its "deep-seated coarse black roots or rootstocks", which when "cut asunder [by ploughing], give rise to new individuals", making it "an unwelcome plant in fields and vineyards." At the time of publication, Greene had a single specimen that was not yet fully in flower, provided by J. A. Sanford, a pharmacist in Stockton. Subsequent collections by Sanford, presumably from the same location, confirm that *L. sanfordii* falls within the current circumscription of *L. californicum*, not *L. junceum*.

Shirley Graham (Missouri Botanical Garden, personal communication) has confirmed that neither of Greene's new species of *Lythrum* has ever been typified. With her encouragement, we do so here. As an initial step, we note that the publication occurred during the period that Greene was a professor at the University of California, after having cut his ties to the California Academy of Sciences following the contentious election of 1887 (Ertter 2000, 2004). Several years later, Greene moved to Washington, D.C., taking some (but not all) of his collections with him; most of these ended up in either Notre Dame University or the National Herbarium at the Smithsonian Institution. After having personally searched the collections of the California Academy of Sciences and Dudley Herbarium (CAS/DS) and UC/JEPS, being provided with images of candidate specimens at the Notre Dame Herbarium (NDG), and checking the digitized collections at the United States National Herbarium (US) online, we have concluded that neither CAS nor NDG have any original material of *L. adsurgens*, and that the original collection on which *L. sanfordii* was based no longer exists. We accordingly hereby designate a lectotype for *L. adsurgens* and a neotype for *L. sanfordii*.

Lythrum adsurgens Greene, Pittonia 2:12. 1889.—LECTOTYPE (designated here): USA, CALIFORNIA, Marin Co., Tiburon, 14 Jun 1886, *Greene s.n.* (lectotype: UC192423; isolectotypes: F, MO).

Greene's protologue indicates that *L. adsurgens* was the prostrate, perennial form of *L. hyssopifolia* that was "Plentiful in low meadow lands adjacent to the salt marshes of San Francisco Bay, especially about West Berkeley." The only extant collections known that were collected prior to publication date are those designated here as lectotype and isolectotypes.

There are also several post-publication collections of *L. adsurgens* by Greene: one in US from West Berkeley, collected in 1891, and three in NDG from "Shell Mound" (NDG34594 on 7 June 1891, and NDG34595 and NDG34956 on 16 July 1895). This is either the well-known Ohlone shell mound (Uhle 1907) in what is now Emeryville (incorporated 1896), where the Shellmound junction of the Berkeley Branch Railroad connected with the line to the San Francisco ferries (Ford, 1977), or the lesser-known one that was destroyed even earlier near the mouth of Strawberry Creek in west Berkeley.

Lythrum sanfordii Greene, Pittonia 2:12–13. 1889.—NEOTYPE (designated here): USA, CALIFORNIA, San Joaquin Co., Stockton, 1890, *Sanford s.n.* (neotype: NDG34598; possible isoneotypes: JEPS2644, JEPS2645, MO2059275, NDG34597, NDG34599).

In the protologue of *L. sanfordii*, Greene stated: "I have my only specimen, and that one not yet well in flower, from a genial and very helpful correspondent, Mr. J. A. Sanford." Either this solitary collection did not survive the 1906 San Francisco earthquake and fire, or else Greene himself discarded the original specimen in favor of better material sent subsequently by Sanford. Of the several Sanford specimens, collected in 1890 and possibly 1891, the NDG sheet labeled in Greene's hand (Barbara Hellenthal, Notre Dame Univ., personal communication) is selected as neotype. The vague dates make it unclear whether the other sheets are in fact isoneotypes, though they are at least authentic material.

The fact that the two specimens at the University of California are in JEPS rather than UC, and that they were already filed as types in spite of the incompatible year of collection, might be evidence that Greene did in fact replace the original collection when better material was available. Jepson was Greene's protégé, and UC/JEPS lore has it that Jepson helped himself to specimens that he felt belonged in his personal herbarium, independent of their source.

POSSIBILITY OF HYBRIDIZATION IN CALIFORNIA *LYTHRUM*

Greene's recognition of additional species of *Lythrum* in California in the late nineteenth century raises some intriguing questions. Although *L. adsurgens* is now treated as a synonym of *L. hyssopifolia,* the latter is referred to only as an annual in its native Europe (e.g., Webb 1968). The latter species is also described as typically erect, although unusual prostrate plants were noted in winter-wet conditions in Crete (Fielding and Turland 2005), where *L. junceum* is the more common species. In contrast, Greene based *L. adsurgens* on plants that were decumbent to prostrate, stoloniferous perennials, and which were also more common than the more typical *L. hyssopifolia* that he considered "something of a rarity" in California.

One possible explanation for this discrepancy is the phenotypic response of *L. hyssopifolia* to the mild, winter-wet conditions of coastal California, perhaps further influenced by the unique growing conditions of salt marsh edges and shellmounds. An intriguing alternate speculation, however, is whether the undeniable success of *L. hyssopifolia* in California might have resulted from hybridization with either *L. junceum* and/or *L. californicum,* as has been suggested for *L. salicaria* and *L. alatum* Pursh (Houghton-Thompson et al. 2005). If so, Greene might have been observing some of the early recombinants, the most successful of which became ancestral to "typical" *L. hyssopifolia* in California. Comparable hybridizations have been well-documented as an evolutionary stimulus (e.g., Abbott 1992; Ellstrand and Schierenbeck 2000); *L. hyssopifolia* is worth further investigation in this regard.

Possible hybridization could also underlie whatever distinctions led Greene to differentiate *L. sanfordii* from *L. californicum,* and furthermore has significant implications for the invasive potential of *L. junceum.* Most non-native species are not invasive, but it is seldom evident which new arrivals are likely to become so. This challenge to early detection is often exacerbated by a time lag between the first appearance of a non-native species and its subsequent explosive spread, possibly following interspecific hybridization (Abbott 1992; Ellstrand and Schierenbeck 2000). Such lags are generally much less than the time since *L. junceum* became established in California, over a century ago. If *Lythrum* species in California are hybridizing, however, then the current limited invasive potential of *L junceum* should not be taken for granted.

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MALACOTHAMNUS ENIGMATICUS (MALVACEAE), A NEW RARE SPECIES FROM THE DESERT EDGE OF THE PENINSULAR RANGE IN SAN DIEGO COUNTY, CA

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ABSTRACT

Malacothamnus enigmaticus K.Morse & T.Chester (Malvaceae) is a new species endemic to the desert edge of the Peninsular Range in San Diego County, California, USA, from the San Ysidro Mountains in the north to the Laguna Mountains in the south. It is the only *Malacothamnus* species in its geographic range, which contains a unique habitat in San Diego County. *Malacothamnus enigmaticus* is morphologically distinct in many inflorescence characteristics from its two most similar species, *M. densiflorus* (S.Watson) Greene and *M. fasciculatus* (Nutt. ex. Torr. & A.Gray) Greene, which are also geographically closest to the new species. A Principal Components Analysis (PCA) of morphological features shows that *M. enigmaticus* is clearly distinct from both *M. densiflorus* and *M. fasciculatus*, and that all three species show the same level of separation from each other. Hence *M. enigmaticus* should be equally recognized at species rank. *Malacothamnus enigmaticus* and *M. fasciculatus* are both distinguished from *M. densiflorus* by their much-higher density of stellate stem hairs, and in most specimens by their shorter stellate hair rays and more numerous stellate hairs on the calyx. *Malacothamnus enigmaticus* is distinguished from *M. fasciculatus* by its longer calyx bracts, and generally by its wider stipular bracts. *Malacothamnus enigmaticus* is a rare species, known from just two ~150 km^2 areas separated by a gap of ~15 km, one in the Laguna Mountains and one in the Pinyon Ridge / Culp Valley / San Ysidro Mountain area. Due to its limited range and small populations, we propose a California Rare Plant Rank of 1B.3 for the species.

Key Words: bracts, *Malacothamnus aboriginum*, *Malacothamnus densiflorus*, *Malacothamnus fasciculatus,* morphology, taxonomy.

Malacothamnus Greene is a genus of shrubs and subshrubs endemic to the California Floristic Province, the adjacent desert transition zone, and a disjunct area of central Arizona having many taxa in common with the California Floristic Province. The genus is well-known as a fire-follower with plants germinating abundantly post-fire, flowering as early as the first year post-fire, and often dying off as soon as three to four years post-fire due to competition with other shrubs (Bates 1963). *Malacothamnus* taxa are notoriously difficult to separate, with "a lack of distinct morphological characters to delineate taxa" complicated by "unclear … taxonomic boundaries among the species … since morphology within species can be highly variable" (Slotta 2004). Furthermore, molecular analysis has so far been unable to distinguish between species (Slotta 2004).

All recent floral treatments (Munz 1974; Beauchamp 1986; Bates 1993; Slotta 2004, 2012; Bates 2015) agree that at least two species of *Malacothamnus* grow in San Diego County, California: *M. fasciculatus* (Nuttall ex Torrey & A.Gray) Greene and *M. densiflorus* (S.Watson) Greene. Bates (1963) was first to recognize a third species from the Laguna Mountains in San Diego County, which he considered indistinguishable from *M. aboriginum* (B.L.Robinson) Greene except for two characteristics of its calyx bracts (called involucral bracts by Bates). Note that the San Diego County Laguna Mountains should not be confused with Laguna Mountain in San Benito County where *M. aboriginum* actually is found. All references to Laguna in this paper refer to the range in San Diego County. A gap of 540 km lies between the San Diego County populations and the closest known *M. aboriginum* specimen in Kings County.

All treatments since Bates (1963) have called the Laguna plants *M. aboriginum*, except for Slotta (2004, 2012). She removed the Laguna plants from the range of *M. aboriginum* but was silent on where they should be placed. The most recent treatment (Bates 2015) says plants "in the Laguna Mountains in San Diego County… *appear* to be *M. aboriginum*" (emphasis added) and that they sometimes have been assigned to *M. densiflorus.*

Only two morphometric analyses of *Malacothamnus* have been done (Benesh and Elisens 1999; Slotta 2004), and neither assessed the Laguna plants. We decided to conduct a similar analysis that included the Laguna plants to resolve their species placement.

Examining specimens of all *Malacothamnus* taxa, we found that the Laguna plants were unique in their combination of inflorescence type, bract characteristics, and pubescence, with morphology most like those closest in range to it: *M. fasciculatus* and *M. densiflorus*. Focusing on these species for comparison, we measured a wide variety of specimens from the full geographic range of *M. densiflorus;* the full range of what was circumscribed as *M. fasciculatus* var. *fasciculatus* by Slotta (2004); all specimens suspected to be similar to the new taxon from the Lagunas, the immediately-surrounding areas, and throughout Baja California (many annotated as *M. aboriginum*); as well as two specimens of *M. aboriginum* from San Benito County. See Fig. 1 for the geographic locations of the measured specimens in the San Diego County area. This paper describes the Laguna plants as a new species, *M. enigmaticus* K.Morse & T.Chester, and uses this name from here forward for maximum clarity.

MATERIALS AND METHODS

Focusing on the reduced set of taxa as noted above, we measured the characteristics found most useful in the previous two morphometric studies, concentrating on the calyx bracts, calyx, stem and leaf pubescence, and inflorescence structure. Additional characteristics not used in previous studies included stipular bracts and glandular hairs. We refined stem hair density from the qualitative measures used in previous studies to a quantitative measure after Principal Components Analysis (PCA) comparison of preliminary data indicated much greater utility of the quantitative measure for taxon delineation. Some measurements remained categorical, such as the number of flowers per stem node which could not be accurately counted without significant damage to many specimens since they are often tightly clustered and overlapping (Appendix 1). Our final set of measurements included 50 characteristics (Appendix 2). Because bract terminology in previous treatments has been inconsistent, vague, and/or confusing, we explicitly define our terms below. We also separately discuss how the stem pubescence was measured.

We measured 152 specimens, of which 71 were gathered from the field (see details below) and 81 were herbarium specimens from SD, UCR, and RSA (see Fig. 1 for the geographic locations of the measured specimens in the San Diego County area). Measured specimens were from Los Angeles, Orange, Riverside, San Benito, and San Diego counties in California, as well as from Baja California, Mexico. Sampled specimens were chosen to represent the maximum morphological variation of each of these taxa, and to give good geographic sampling of each taxon. Specimens without mature measurable calyxes and bracts were avoided as were a few with significant damage to the stem hairs. Some collections from the same plant and/or population were measured to show variation within each.

Field Work

We surveyed for *Malacothamnus* on 52 separate days from 13 February 2015 to 14 December 2017 to find and study plants in the field. We made 128 specimen collections on 28 separate days. In many cases, we took three or more separate sheets at a given location to represent the maximum morphological variation at a site, usually the least and most robust inflorescences as well as a typical one, sometimes all from the same plant. Several field trips were devoted to delineating the distribution of *M. enigmaticus*, with four trips specifically made to record its characteristics in the field, where we assessed the habitat and measured plant size, shape/form, and lower leaves, characteristics that cannot be assessed from herbarium specimens.

Details on the Measured Characteristics – Bract Terminology

There has been general agreement that there are leaves (sometimes called leaf-like bracts) subtended by stipules in the *Malacothamnus* inflorescence, and that the calyx is subtended by a whorl of three bracts that have been given various names by different authors. However, the intervening bracts are not clearly defined in any of the previous treatments. In this section, we define the terminology we use in this paper. Our terminology is simplified from previous authors in the hopes of reducing confusion. See Fig. 2 for a labeled diagram illustrating the terminology we are using.

Directly below the calyx are three bracts forming a whorl (Fig. 2A and 2B). These have collectively been called the involucel or epicalyx. Individually they have been called bracts, bractlets, bracteoles, involucral bracts, involucellar bractlets, and involucellar bracteoles. We call them an involucel made up of three calyx bracts.

Leaves in *Malacothamnus* generally decrease in size distally and fairly large single leaves can often be found in the inflorescence, one at each node. Technically, leaves in the inflorescence are bracts, but there is often no clear line in *Malacothamnus* where leaves end and leaf-like bracts start. A new inflorescence branch may begin at any of the uppermost leaves. This often makes the boundary between inflorescence branches and axillary inflorescences unclear. Since there already are an abundance of bract types in the inflorescence, for clarity we call them leaves if they look like leaves, have stipules, and are unmodified from the lower leaves beyond reduction in size. *Malacothamnus palmeri* (S.Watson) Greene is the only species in the genus to have leaves in the inflorescence that are modified in shape as well as size; we call those "leafy bracts".

Subtending each leaf is a pair of stipules which are often leafy, but sometimes reduced to scales. Occasionally these stipules are basally fused in the distal end of the inflorescence. Vestigial leaves may be found with the more-proximal fused stipules, but

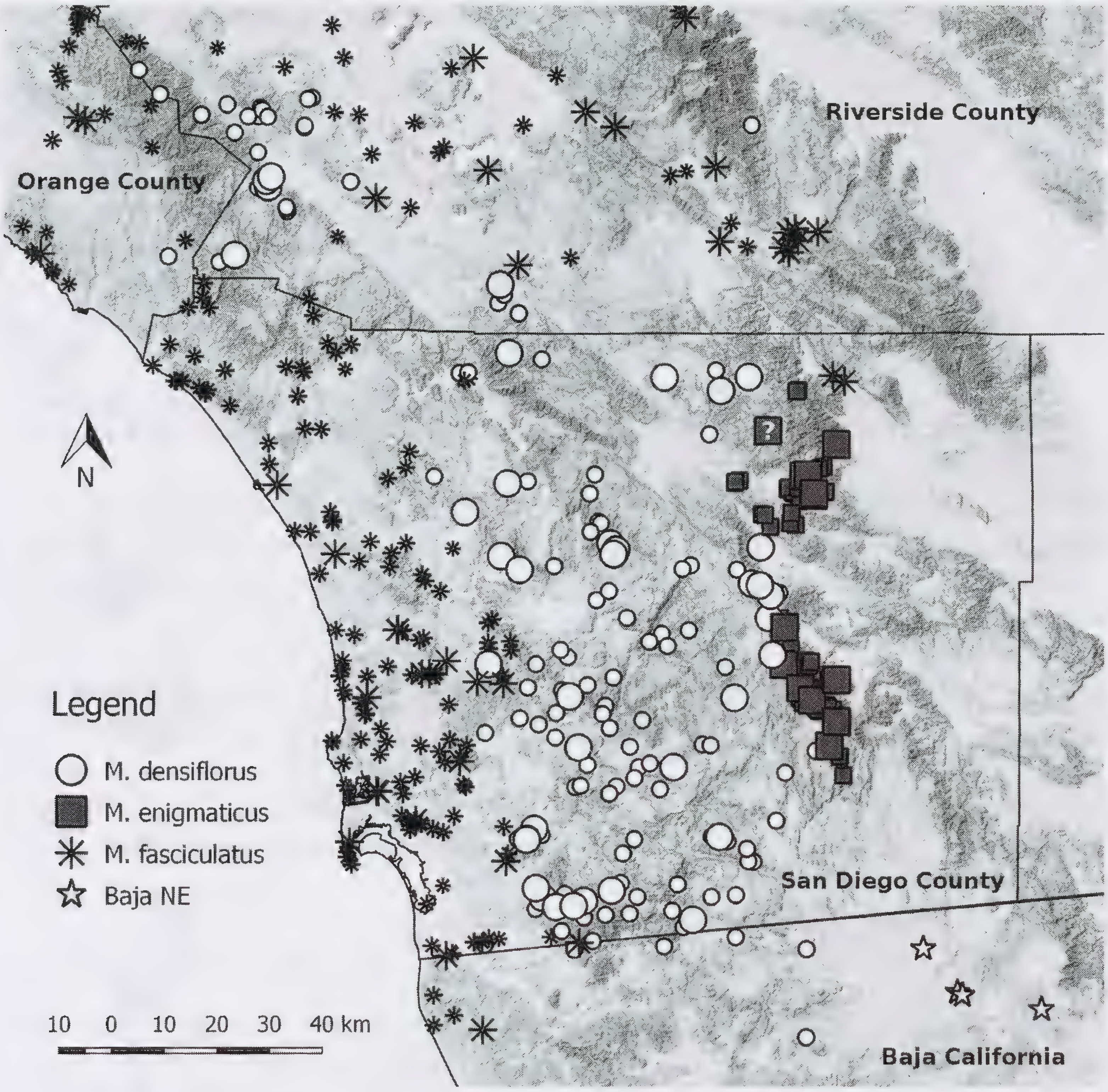

FIG. 1. The full geographic range of *M. enigmaticus* (filled squares), along with nearly the full geographic range of *M. densiflorus* (open circles), and the nearby portion of the range of *M. fasciculatus* (asterisks). Measured and analyzed specimens are shown with larger symbols. *Malacothamnus enigmaticus* likely exists at or near the single location marked with a question mark (see text). The *Malacothamnus* specimens in northeast Baja California (open stars) appear to differ from each of these three species, but too few specimens are known to generate reliable conclusions.

often only persist for a few nodes. Hill (1982) noted this in the related genus *Malvastrum*:

> "In many individuals a progression can be clearly seen from well-developed leaves with associated stipules, to reduced leaves with stipules, stipules with a leaf remnant attached, and finally to a bifid bract."

This is illustrated in Fig. 2D. When a bifid bract is present at the base of a node on the main inflorescence axis in the stipular position, we call these "fused stipules".

At a given node, additional bracts resembling stipules or fused stipules are often present between the stipules and the calyx bracts. These bracts have not been clearly defined in any *Malacothamnus* treatment. In Malvaceae, similar bracts have been called floral bracts, stipular bracts, and/or inflorescence bracts (S. Hill, University of Illinois, personal communication). Here we use the term "stipular bracts". In *M. enigmaticus,* clusters of stipular bracts subtend clusters of flowers in the inflorescence. The shape of these stipular bracts can vary considerably even within a single glomerule of the inflorescence (Fig. 2C and 2E).

Details on the Measured Characteristics – Hairs

Malacothamnus hairs often change along the stem, especially near the distal end of the inflorescence where they may be sparser, longer-rayed, and/or more stipitate. For consistency and to avoid disparity in developmental maturity at the distal end of the inflorescence, we measured the stem hairs near the proximal end of what is generally found on specimens. We measured stem hair type (stellate or simple glandular), density, length of stellate hair rays, length of stellate hair stipes, and length of glandular hairs.

Stellate stem hair density was sampled in a 2.0 × 2.0 mm square where the stem was 2–4 mm (generally 3 mm) in diameter. The square we actually used for measurement was 2.0 × 2.3 mm. To avoid confusion, we refer to it as a 2 × 2 mm square in this paper, and all numbers given here were scaled from the actual measurements by multiplying by 2.0 / 2.3.

Condition and size of the specimen, as well as ease in accessing a sampling location, often influenced where we measured the stem. Areas where hairs were damaged, or not typical of that region of the stem, were avoided. A card with a 2 × 2 mm square hole

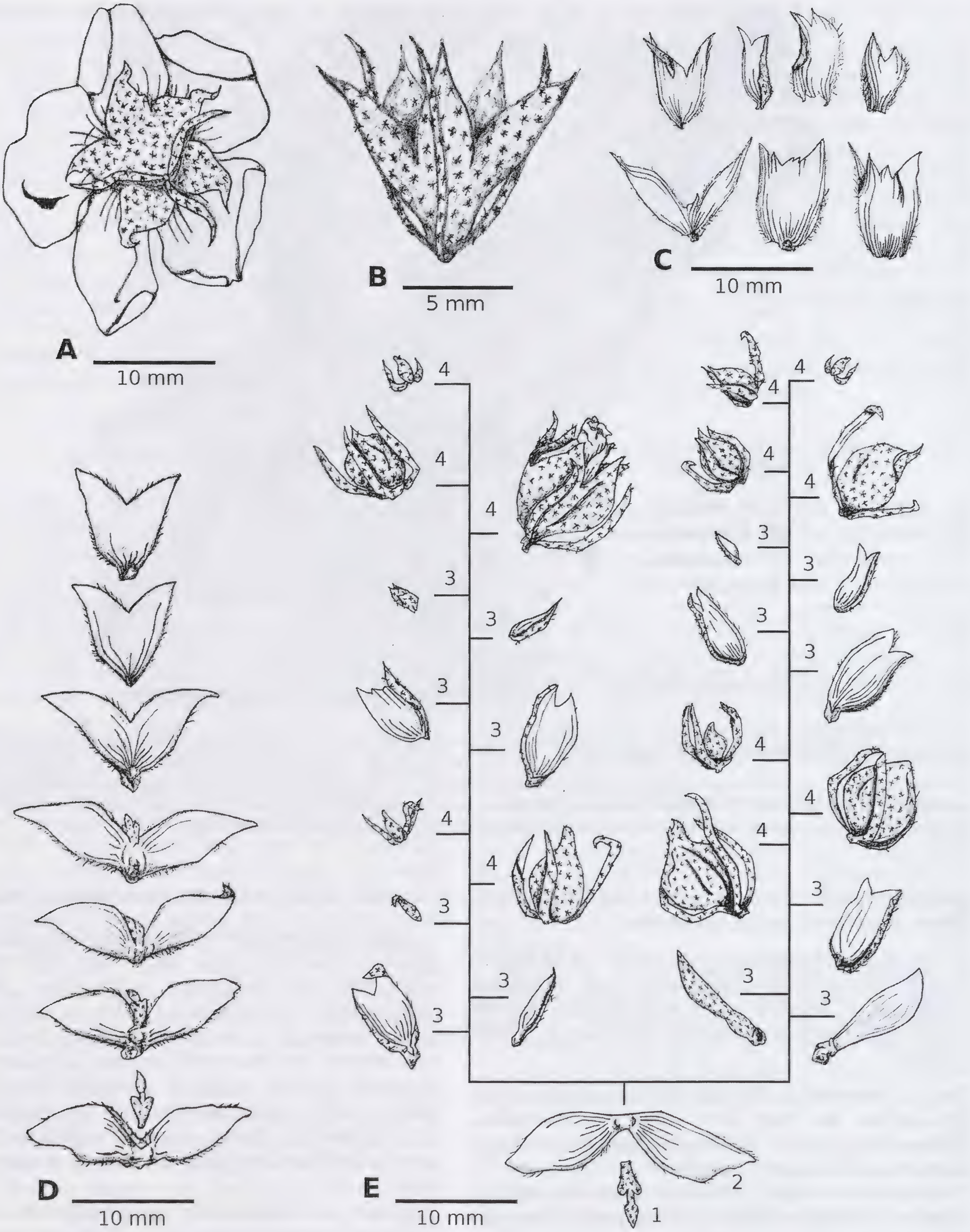

FIG. 2. *Malacothamnus enigmaticus* bracts and a dissected glomerule. A. Basal view of flower showing calyx and the three subtending linear calyx bracts. B. Side view of calyx and calyx bracts. C. Some variation in stipular bracts. D. Transition from stipules with reduced leaf (bottom/proximal) to fused stipules (top/distal). E. Example of a dissected glomerule with a reduced leaf (1) and stipules (2) at the base transitioning to two reduced branches with alternating clusters of stipular bracts (3) subtending clusters of flowers (4). The calyx bracts are shown attached to the calyx. Illustrations by Elysa DuCharme.

was placed over the sample area, the hairs were gently scraped off within this square, and then counted on another surface. In some species, such as *M. fasciculatus* and *M. enigmaticus*, the hairs may be very small and in densely-overlapping layers. In these cases, care was taken to try and remove as many individual hairs as possible (rather than removing clumps). When scraped off in clumps, hairs can be much more difficult to separate and count.

Stem stellate hair rays were measured from the 2 × 2 mm sample and surrounding areas. Stem stellate hair stipes were measured from the areas on the stem immediately surrounding the 2 × 2 mm sample area. When scraped, the stipes often broke above the base, so stipes were only measured for hairs still attached to the stem. Stem glandular hair length was measured near the 2 × 2 mm sample area, but with more flexibility in distance in order to record a greater range of hair lengths, as they were much sparser than the stellate hairs.

The stem hairs from a representative specimen of each of the four species analyzed were also examined with a scanning electron microscope (SEM). Stem sections of the selected species were mounted on aluminum stubs using conductive tape, coated with gold using a Cressington Sputter Coater 108auto system (Cressington Scientific Instruments, Watford, UK), and imaged on a Hitachi SU3500S Variable Pressure SEM (Hitachi High Technologies America, Inc., Pleasanton, CA) at Rancho Santa Ana Botanic Garden.

Principal Components Analysis

Our fundamental analytical tool was a principal components analysis (PCA) performed using the *princomp* function in R (R Core Team, R Foundation for Statistical Computing, Vienna, Austria), which removes the mean from each measurement, and then divides the result by its standard deviation. A PCA is a powerful tool to analyze a dataset composed of numerous measurements of a large number of specimens to easily visualize whether the specimens group into separate taxa or not; see, e.g., Keeley et al 2007. A PCA linearly transforms a dataset with multiple, usually highly correlated, variables into a new set of uncorrelated variables ranked in order of how much variance in the dataset is encompassed by each variable in turn. Typically, most of the variance in the data is explained by the first few "principal components", allowing easy visualization of the structure of the original data set using just a few variables. Another advantage of a PCA is that it is an unbiased approach, weighting all measured characteristics equally, to studying whether multiple species are supported by the data, in contrast to selecting "key" characteristics which may or may not be supported by differences in other characteristics.

We began our analysis after measuring just 19 characteristics on the first 15 specimens. We used the preliminary analyses to guide us in selecting additional characteristics to measure and in selecting additional specimens to measure. We strove to sample all the variation we saw in the voucher specimens we examined and, as detailed above, in the plants in the field. It proved very useful to have multiple measured specimens from the same plant to provide a quantifiable baseline of variation within a single species. This drove us to measure additional characteristics, and/or to sharpen our measurements of some characteristics, to try to separate the species more cleanly. We also found that the inflorescence length and the lengths of the internodes above the most proximal internode were not useful in separating the species and eliminated them in the PCA. Those lengths are heavily influenced by the timing of the collections since the distal internodes elongate much later than proximal internodes. We retained the length of the most proximal internode since it matures first and is fairly consistent in each species.

We initially analyzed all specimens of all species together, but soon found that it was better to analyze just two or three species at a time, especially those in a given geographic area, since a plot of the first two PCA components readily discriminates two or three species, but often produces significant overlaps with more species.

RESULTS

Visual comparison of specimens of *M. enigmaticus* to the rest of genus found *M. enigmaticus* to be most similar in morphology to *M. densiflorus* and *M. fasciculatus,* rather than to *M. aboriginum* as suggested by Bates. Bates (1963) considered *M. aboriginum* indistinguishable from *M. enigmaticus* with the exception of the calyx bracts being "mostly 2–9 mm broad and often connate basally" in *M. aboriginum* compared to "rarely more than one millimeter broad and free" in *M. enigmaticus.* While both *M. aboriginum* and *M. enigmaticus* are united in the uncommon characteristic of wide stipular bracts, which may have caused Bates to place them together, they are widely divergent in two other important characteristics: pubescence type and calyx lobe shape. *Malacothamnus aboriginum* has large and sparse stellate hairs with very wide, subcordate calyx lobes, whereas *M. enigmaticus* has minute and dense stellate hairs with much narrower, ovate calyx lobes.

Scanning electron micrographs of representative stem hairs of the three San Diego County *Malacothamnus* species and *M. aboriginum* from San Benito County are shown in Fig. 3. *Malacothamnus enigmaticus* and *M. fasciculatus* have a relatively-high density of hairs (Fig. 3A and 3B). In and near San Diego County, the stellate hair rays are often longer in *M. fasciculatus* than *M. enigmaticus*, but more northern and higher elevation *M. fasciculatus* are comparable to *M. enigmaticus* in ray length. *Malacothamnus densiflorus* and *M. aboriginum* have a relatively low density of hairs (Fig. 3C and 3D). Note that the ray length of *M. aboriginum* vastly exceeds those of the other taxa (Fig. 3D).

As expected, the PCA with all species together showed significant separation of *M. aboriginum* from the remaining species (Fig. 4). Hence *M. aboriginum* was excluded from all additional PCAs. In this PCA with all species together, PCA1 accounts for 32% of

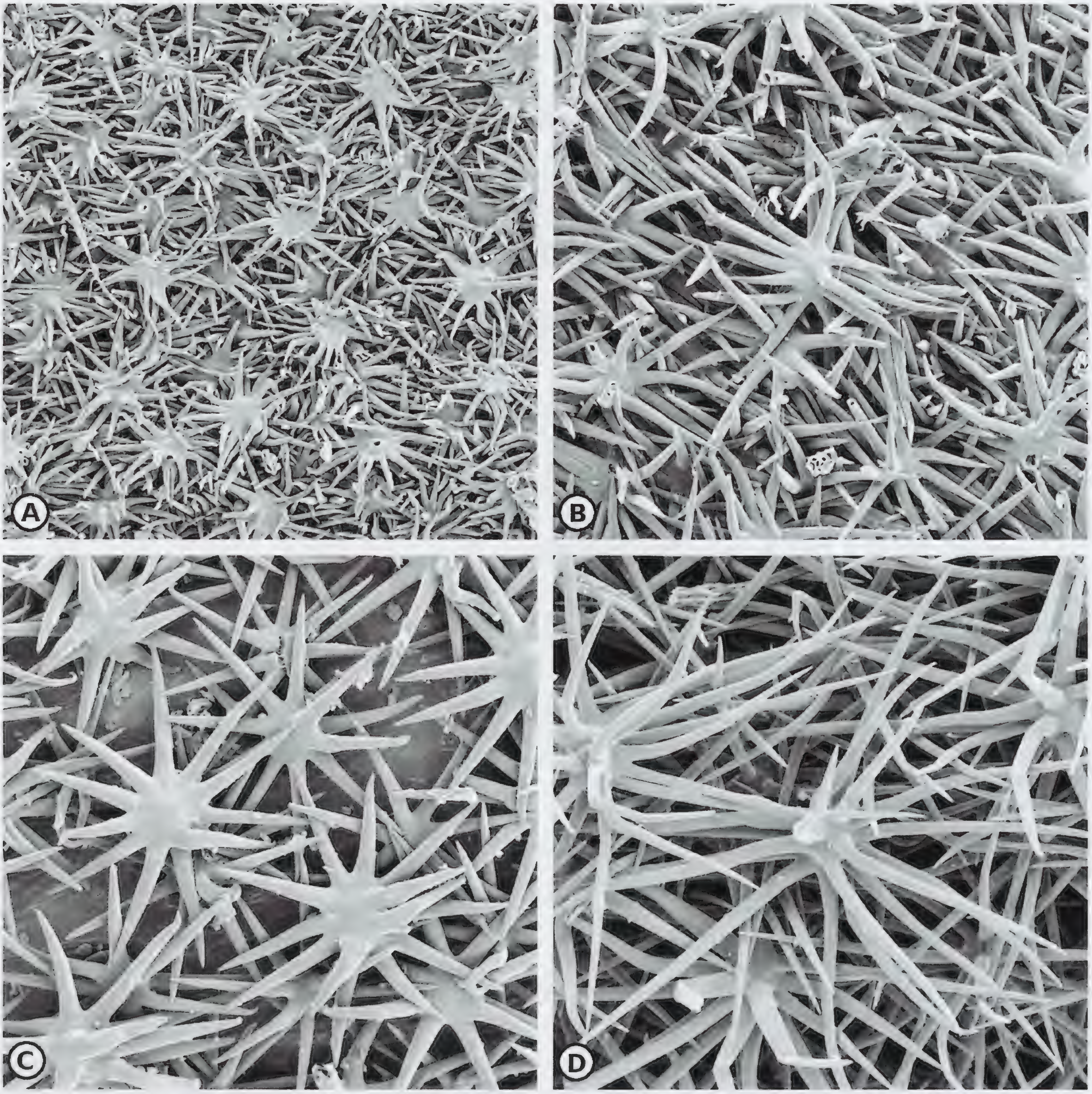

FIG. 3. Scanning electron micrographs showing a 1 × 1 mm square of stem hairs near the base of the inflorescence typical of the three San Diego County *Malacothamnus* species and *M. aboriginum* from San Benito County (Photo: K. Morse). A. *M. enigmaticus* (Morse M023). B. *M. fasciculatus* var. *fasciculatus* (Morse M007). C. *M. densiflorus* (Morse M020). D. *M. aboriginum* (Morse M110).

the total variance; PCA2 for 13%; and PCA3 for 9%. PCAs not shown indicated some specimens in Baja California are possibly undescribed taxa which need further sampling to adequately assess. As a result, these Baja California specimens were not used in the PCAs shown here.

The PCA results of the 138 remaining specimens (Fig. 5) and the geographic map (Fig. 1) indicate that M. enigmaticus is clearly distinct from *M. densiflorus* and *M. fasciculatus* both morphologically and geographically. The PCA separation is robust and comes from many different characteristics; half of the coefficients for the first Principal Component (PCA1) in both analyses are within a factor of two of the largest coefficient (Appendix 2). Those 138 specimens span the full range of *M. enigmaticus* and *M. densiflorus*, as well as the full range of what is circumscribed as *M. fasciculatus* var. *fasciculatus* in Slotta (2004), excluding what appear to be undescribed taxa in Baja California.

The morphological separation of *M. enigmaticus* and *M. densiflorus* (Fig. 5A) is especially good, with a gap between all members of each of the species in the PCA plot. Furthermore, the PCA shows that the set of measured plants of *M. enigmaticus* is homogeneous, since the dispersion in the PCA values for *M. enigmaticus* is essentially the same as the dispersion in the PCA values of three samples from one plant (the

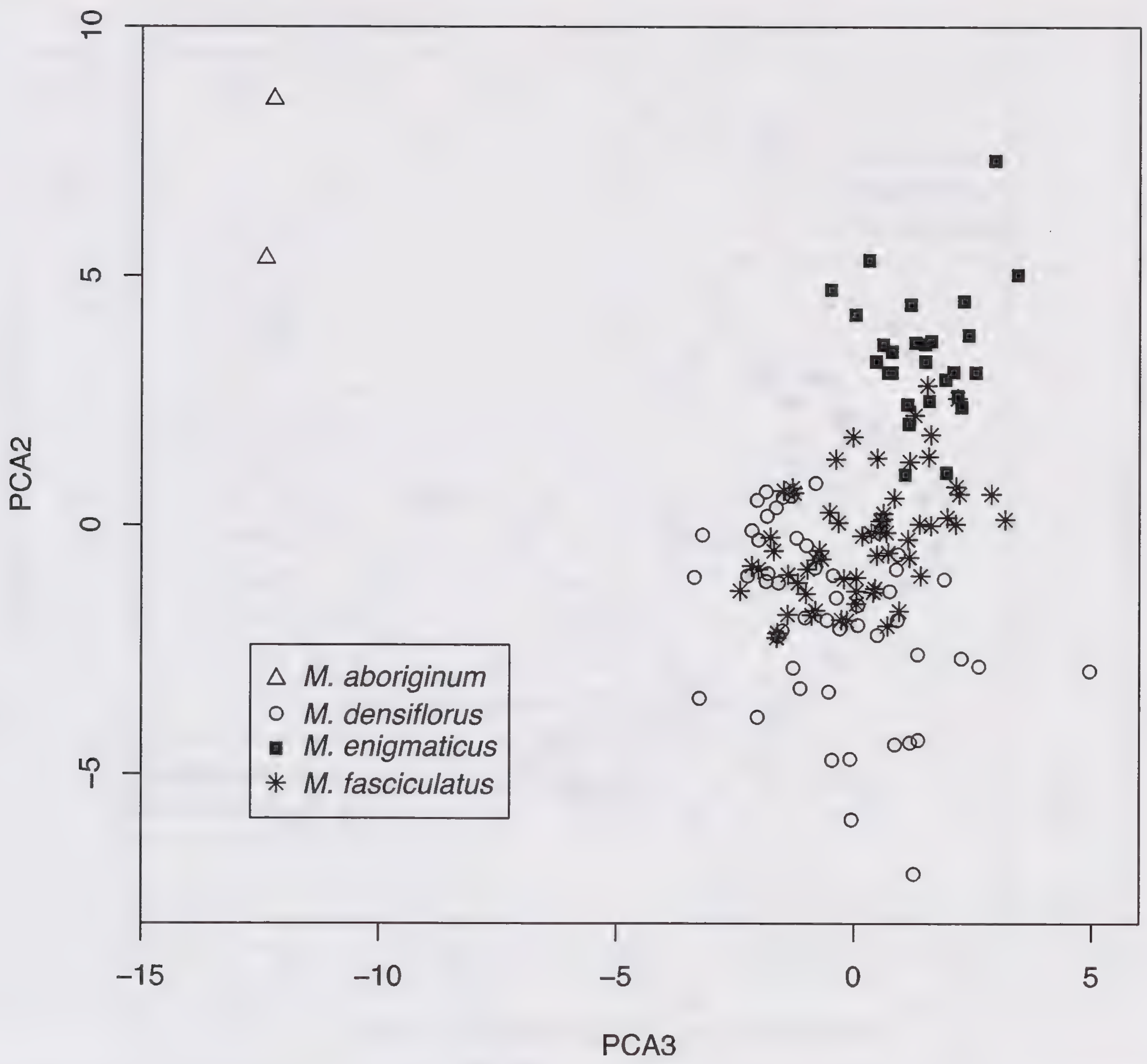

FIG. 4. Principal Component Analysis using all 50 measured characteristics for 140 *Malacothamnus* specimens, 138 from the San Diego County area northward to Los Angeles and San Bernardino counties, plus two specimens of *M. aboriginum* from San Benito County. The unique characteristics of *M. aboriginum* were best captured by the third principal component, where it is separated from the other three species by roughly 13 standard deviations.

diamond points in the plot). These samples were intentionally chosen to represent the extreme amount of variation within a single plant (more than typical), as we wanted to compare those values across the PCA plot. A separate PCA using only *M. enigmaticus* specimens (not shown here) produced the spherical cloud of points, with no geographic trend, expected if the species is homogeneous.

In contrast, *M. densiflorus* is heterogeneous. The samples from the same plant (Fig. 5A, the points with separate symbols in the plot) occupy only a small range of the variance in its PCA. A separate PCA using only *M. densiflorus* specimens (not shown here) shows clear trends with geography, which roughly correlates with its two previously recognized varieties and possibly a third undescribed taxon.

The presence of subtaxa within *M. densiflorus* skews the PCA plot in Fig. 5A such that the two species are separated along a diagonal in the plot. If only two species were present, each of which is homogeneous, they would be primarily separated along the PCA1 axis.

The morphological separation of *M. enigmaticus* and *M. fasciculatus* (Fig. 5B) is excellent. Again, *M. enigmaticus* is seen to be homogeneous, even though it is spread over quite a range in PCA1 values, since the separate samples from the same plant span almost the full range of PCA1 values for the specimens sampled.

Malacothamnus fasciculatus is heterogeneous, again seen from the samples from the same plant occupying only a small range in its variance in PCA1 and PCA2 (Fig. 5B). A separate PCA using only *M. fasciculatus* specimens (not shown here) shows clear trends with geography. Although the trends do not seem to correlate with previously defined varieties of the species, they indicate that there is variation within *M. fasciculatus* that may warrant further circumscription.

The presence of subtaxa within *M. densiflorus* and *M. fasciculatus*, and the resulting different structure of the two PCA plots in the comparison of each with *M. enigmaticus*, accounts for the difference in variance explained by the first two principal components. PCA1 accounts for 38% of the total variance between *M. enigmaticus* and *M. fasciculatus*, cleanly separating the taxa with just PCA1 (Fig. 5B). In comparison, PCA1 accounts for just 24% of the total variance between *M. densiflorus* and *M. enigmaticus*, since the separation is along a diagonal line relating PCA1 and PCA2 (Fig. 5A). The total variance accounted for by both PCA1 and PCA2 combined is similar in the two PCAs, 47% for *M. enigmaticus* and *M. fasciculatus* and 43% for *M. densiflorus* and *M. enigmaticus*. This total variance is much higher than that from a random distribution derived from the broken-stick model (Jackson 1993); the broken-stick model gives that the variances of the first nine PCA components are better than expected from

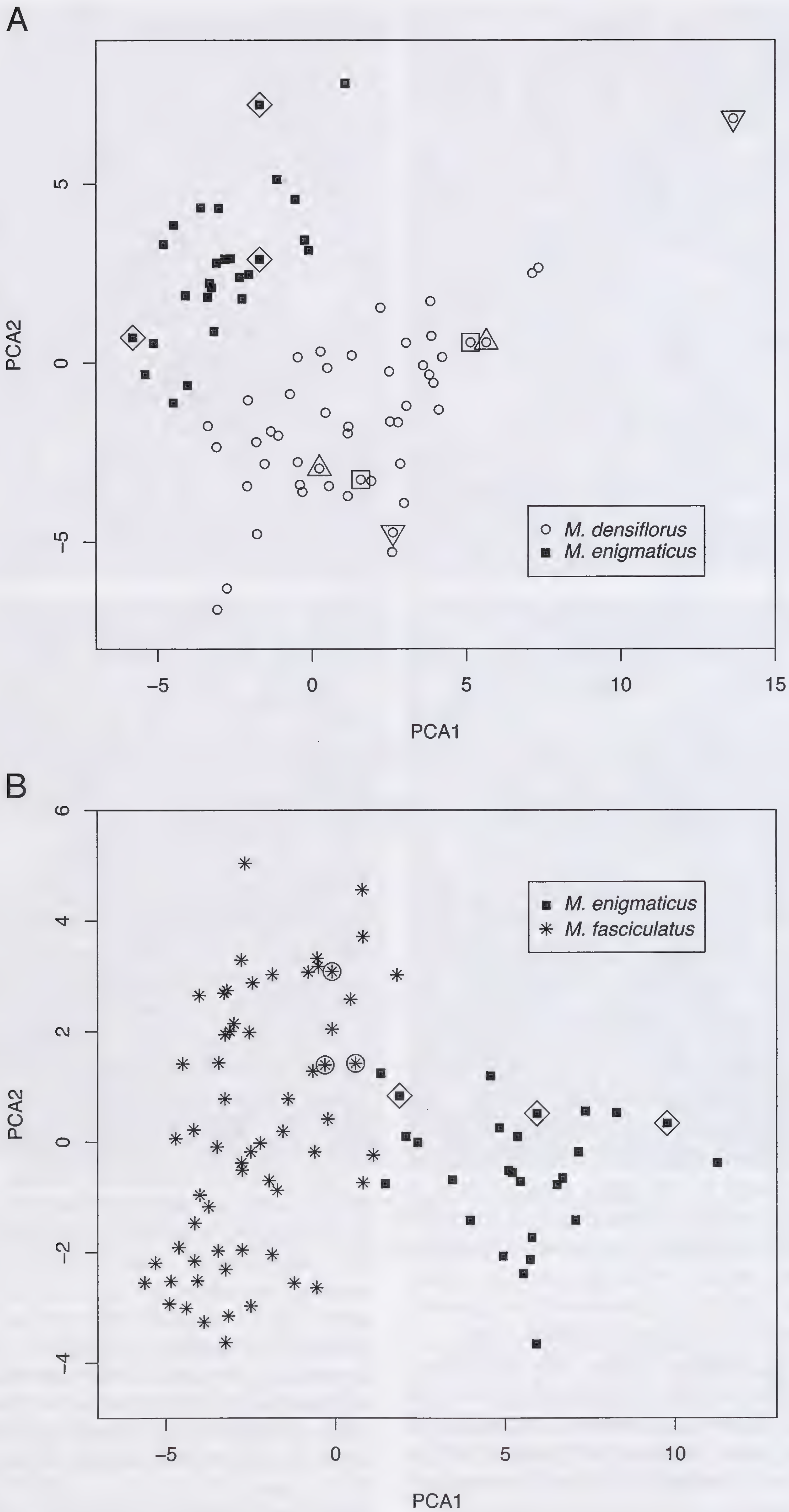

FIG. 5. Principal Component Analysis (PCA) for 138 *Malacothamnus* specimens from the San Diego County area northward to Los Angeles and San Bernardino counties. A: PCA using all 50 measured characteristics for only specimens of *M. densiflorus* and *M. enigmaticus*. B: PCA using 44 measured characteristics for only specimens of *M. enigmaticus* and *M. fasciculatus* (the other six measured characteristics were identical for all specimens of these two species). The points for specimens from the same population, and sometimes the same plant, where we intentionally sampled the extreme morphological variation with multiple specimens, are marked with additional symbols that are unique for each population, such as the diamonds surrounding the three *M. enigmaticus* data points that come from the same plant.

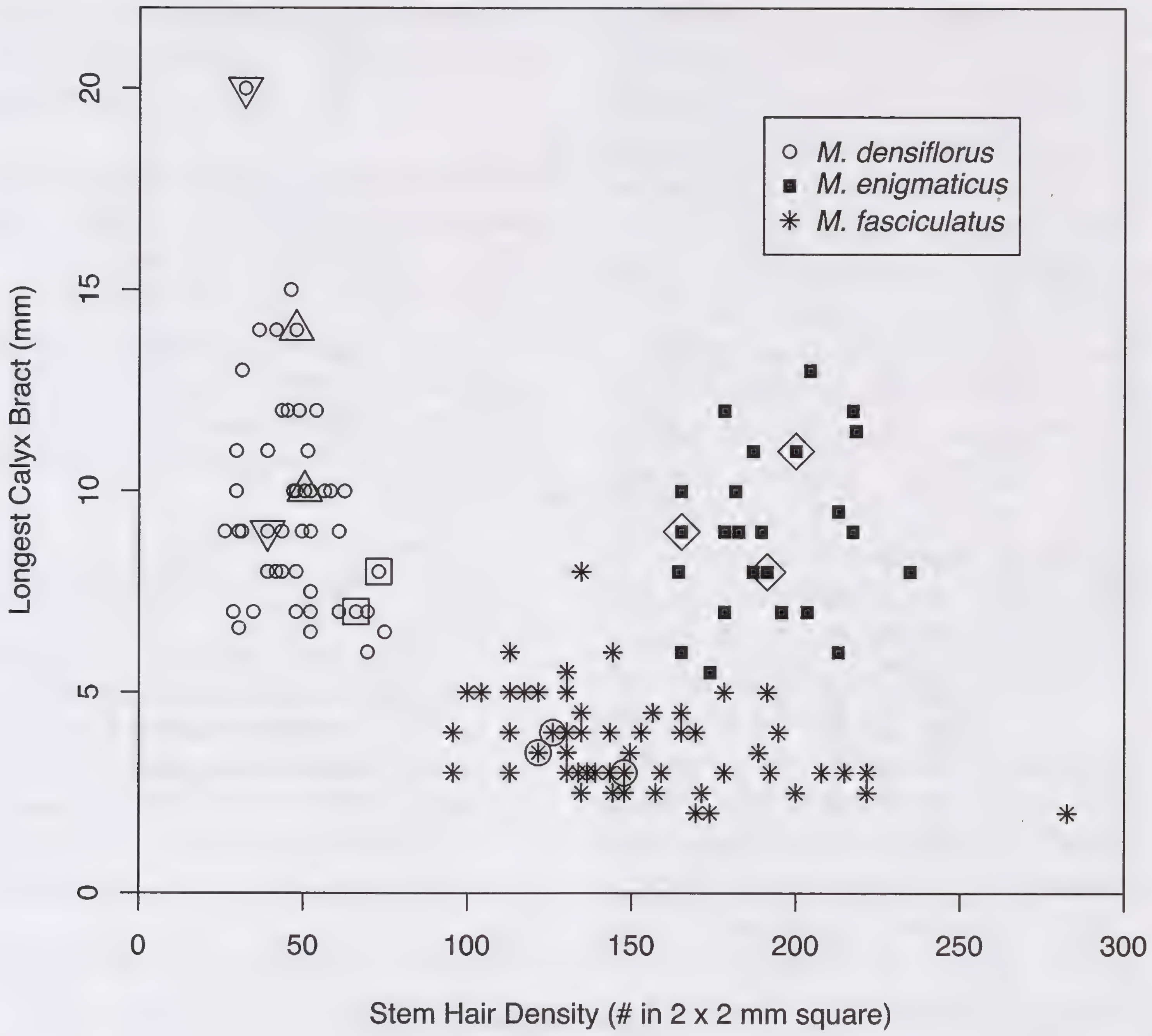

FIG. 6. Plot of the longest calyx bract in each specimen vs. the density of stem hairs. This plot, using just two characteristics, essentially reproduces the separation of the three species from the PCA with 50 characteristics.

chance for the *M. enigmaticus* and *M. fasciculatus* analysis, and the variances of the first 11 components are better than expected from chance for the *M. densiflorus* and *M. enigmaticus* analysis.

The PCA plot shows that some specimens of *M. enigmaticus* are close to some specimens of *M. fasciculatus* in the values of PCA1 and PCA2. However, the taxa are cleanly separated in some higher-order PCA components, are disjunct geographically, and they are readily distinguished using the key presented in this paper. Hence their species assignment is unambiguous. In fact, one of those specimens of *M. enigmaticus* has two other samples from the same plant plotting in the middle and farthest part of the *M. enigmaticus* distribution relative to *M. fasciculatus* (see the specimens represented with diamonds in Fig. 5B).

The PCA coefficients from the PCA using all three species show that the most-important separating characteristics of the three species are stem hair density, the length of the longest calyx bracts, and the width of the widest stipular bracts. The longest calyx bract in each specimen is plotted vs. the density of stem hairs in Fig. 6, showing that the three species separate quite well just using two measured characteristics. The widest stipular bract is plotted vs. the longest calyx bract in Fig. 7 for *M. enigmaticus* and *M. fasciculatus*, showing the excellent separation of those two species using just two characteristics.

The majority of the measured characteristics show strong differences in their mean values between at least two of the three species. The means for 39 characteristics differ between at least two species at the five standard deviation level or higher, with 19 of those above the ten standard deviation level. The strongest discriminant is the stem hair density, with the mean values for *M. densiflorus* and *M. fasciculatus* differing by 21 standard deviations; *M. densiflorus* and *M. enigmaticus* differing by 35 standard deviations; and *M. fasciculatus* and *M. enigmaticus* differing by seven standard deviations.

Table 1 provides some of the most important characteristics that separate *M. densiflorus*, *M. enigmaticus,* and *M. fasciculatus,* and the range of our measurements for each species. The measurements came from 49 specimens of *M. densiflorus*, 27 specimens of *M. enigmaticus,* and 62 specimens of *M. fasciculatus.* More *M. densiflorus* and *M. fasciculatus* specimens were measured since those two species have a much larger geographic range and more morphological variation than does *M. enigmaticus*, possibly due to the presence of subtaxa within those two species (See Figshare Data Repository measurements on these specimens, https://doi.org/10.6084/m9.figshare.8061692).

Several significant distinguishing features in categorical measurements were found. The density of hairs on the sepals and leaves averaged one category lower in *M. densiflorus* than in the other two species. The presence of glandular hairs greater than or equal to 0.1 mm on the stem only occurs in one possible subtaxon of *M. densiflorus. Malacothamnus densiflorus sensu stricto (s. s.*), which has populations closest in range to *M. enigmaticus*, has sparse hairs near the base of the calyx, whereas *M. fasciculatus*,

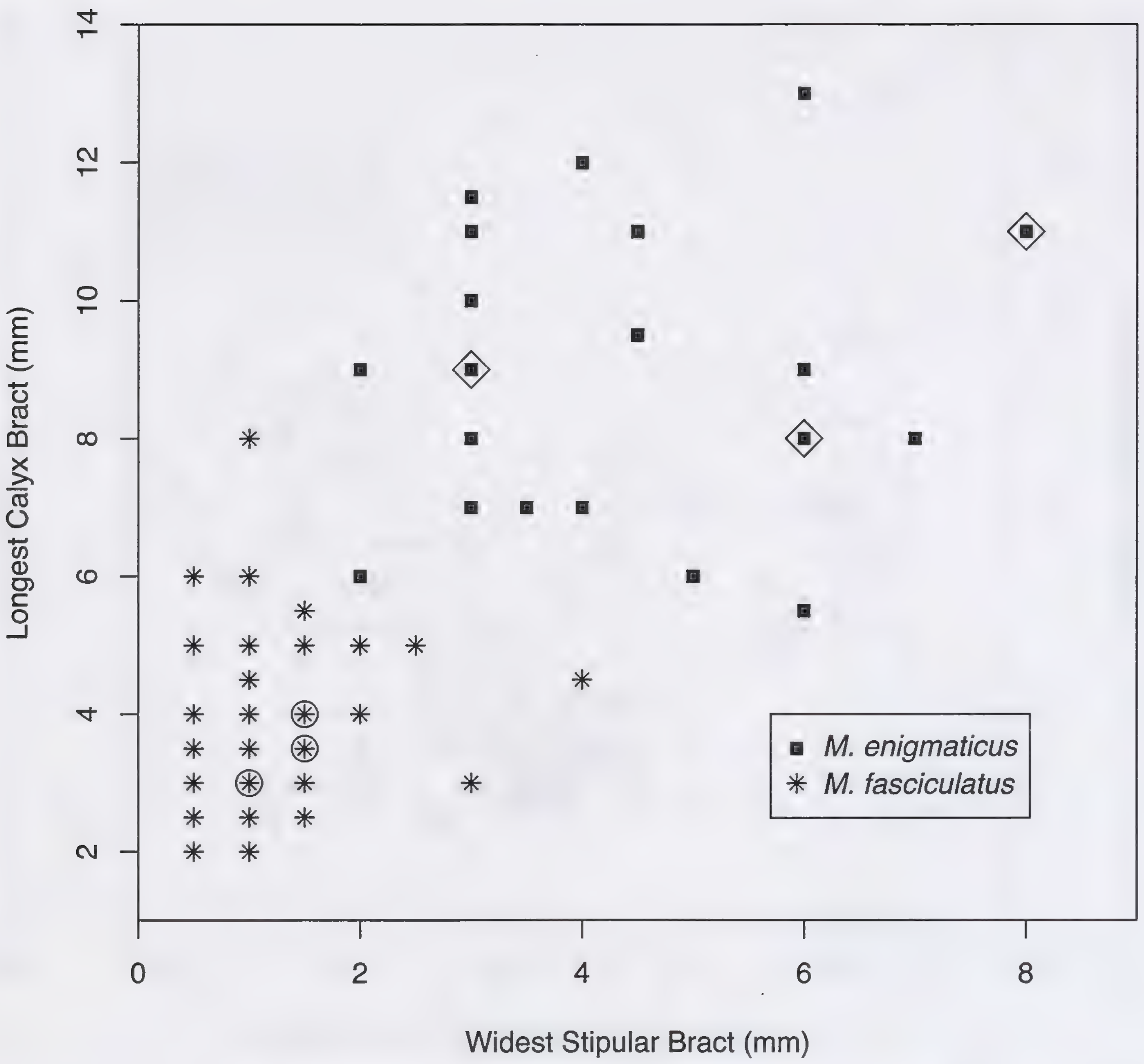

FIG. 7. Plot of the longest calyx bract vs. widest stipular bract for *M. enigmaticus* and *M. fasciculatus*. This plot, using just two characteristics, essentially reproduces the separation of the two species from the PCA with 50 characteristics.

M. enigmaticus, and the other possible subtaxa of *M. densiflorus* have dense hairs.

CONCLUSION

Malacothamnus enigmaticus is taxonomically distinct and merits designation at the rank of species. It occurs with no other *Malacothamnus* taxa and consists of a morphologically-homogeneous group of plants with a well-defined geographic range occupying a unique habitat in San Diego County, where the eastern edge of montane elevations transition rapidly to the low desert. It is morphologically distinct from all other *Malacothamnus* species in its unique combination of inflorescence type, bract characteristics, and pubescence, with morphology most like those closest in range to it, *M. fasciculatus* and *M. densiflorus.*

The separation of *M. enigmaticus* from these species is robust. It is cleanly distinguished using just two characteristics. Furthermore, it is clearly distinguished in a PCA even when the PCA is restricted to using various independent subsets of the measured characteristics, showing that it is distinct from those species in a number of characteristics.

TABLE 1. IMPORTANT CHARACTERISTICS SEPARATING *M. DENSIFLORUS*, *M. ENIGMATICUS,* AND *M. FASCICULATUS.* Values in bold type indicate characteristics significantly different (exceeding two standard deviations) from those of the other two species. [1] The median value varies in the different possible subtaxa [2] Longest-rayed stellate hairs are generally sparsely scattered on the stem in these three species.

	M. densiflorus			*M. enigmaticus*			*M. fasciculatus*		
Characteristic	min	median	max	min	median	max	min	median	max
Stem hair density # per 2 × 2 mm square	**26**	**48**	**75**	164	187	235	96	143	283
Stem stellate hair stipe length (mm)	0	**0.1**	**0.4**	0	0	0	0	0	0.2
Stem stellate hair ray length (mm)	0.1	**0.2–0.3**[1]	**4.1**[2]	0.1	0.1	0.5[2]	0.1	0.1–0.2[1]	1[2]
Most proximal infl. internode length (mm)	12	58	**130**	20	51	75	**8**	**30**	75
Stipular bract width (mm)	0.5	0.7	3.0	0.5	**3.0**	**8.0**	0.5	0.7	4.0
Calyx bract length (mm)	5	8	**20**	3	8	13	**1**	**3**	**8**
Calyx bract hairs longest average (mm)	0.5	1.5	**3.0**	0.5	1.0	1.5	0.5	0.5	1.0
Calyx length (mm)	6.0	10.3	**21.0**	6.0	10.0	15.0	5.0	**7.4**	**10.0**
Calyx lobe length (mm)	3.0	6.3	**13.5**	3.0	6.3	10.0	**1.5**	**3.7**	**7.0**
Calyx lobe width (mm)	2	3.5	5.5	2	3.7	5	2	3	4
Longest calyx hair rays (mm)	**1.0**	**2.0**	**4.0**	0.5	1.0	2.0	**0.3**	**0.4**	**1.0**

TAXONOMIC KEY TO THE SPECIES OF *MALACOTHAMNUS* IN SAN DIEGO, ORANGE, AND RIVERSIDE COUNTIES, CA

The following key unambiguously separates all the specimens measured for this paper despite the small overlap in each of the two characteristics used to separate *M. fasciculatus* and *M. enigmaticus* (Figs. 6 and 7). Stem hairs are measured near the base of the inflorescence where the stem is 2–4 mm wide. Stipular bracts are most easily seen proximally in glomerules, especially when flowers are immature (Fig. 8D).

1. Stem hairs 26–75 in a 2 mm x 2 mm square, green stem generally visible to the naked eye between hairs . . . . *M. densiflorus*

1′ Stem hairs 164–235 in a 2 mm x 2 mm square, stem yellow or white due to densely overlapping hairs, green stem rarely visible distally 2

2. Longest calyx bracts 2.5–6.0 mm; widest stipular bracts 0.5–2(4) mm wide . . . . *M. fasciculatus*

2′ Longest calyx bracts 5.5–13 mm; widest stipular bracts 1–8 mm wide . . . . *M. enigmaticus*

We did not include Baja California in the key since *M. densiflorus* and *M. fasciculatus s.s.* do not extend very far south of the San Diego County border. Our analyses indicate much of what has been called *M. densiflorus* and *M. fasciculatus* in Baja California may differ from those species and requires further investigation.

To the north of the region of this key, Los Angeles, San Bernardino, Santa Barbara, and Ventura counties all have *M. fasciculatus*. A sampling of additional specimens of *M. fasciculatus* from this area all fit within the key. These counties were left out of the key due to currently-unresolved morphological differences between *M. fremontii* (Torr. ex A.Gray) Greene and *M. orbiculatus* (Greene) Greene.

TAXONOMIC TREATMENT

Malacothamnus enigmaticus K.Morse & T.Chester, sp. nov.—Type: USA, California, San Diego County, Laguna Mountains, southernmost hill in Garnet Peak vicinity, in sandy soil of disturbed chaparral (fuel break); 32.909°N, –116.463°W, 1650 m, 23 June 1977, Fred T. Sproul 170 (holotype: SD114895).

Bract terminology used here is explicitly defined in the Materials and Methods section and illustrated in Fig. 2. See Fig. 8 for photographs illustrating some of the characteristics mentioned below.

Distinguished from *M. densiflorus* by its much-higher density of stem hairs, 164–235 in a 2 mm x 2 mm square near base of inflorescence where the stem is 2–4 mm wide, vs. 26–75. Distinguished from *M. fasciculatus* by its longer calyx bracts, longest ones in inflorescence 5.5–13 mm compared to 2.5–6.0 mm, and by its wider stipular bracts, widest ones in inflorescence 2.0–8.0 mm, vs. 0.5–2(4) mm.

Shrub to 2.1 m tall and 2.4 m wide, generally slightly wider than tall and approximately hemispheric in shape; occasionally height 2–3× width, especially in young plants and those with lowest branches herbivorized; mostly branched from near base without clear central stem; occasionally with clear central stem, but still with most larger branches from near base; very rarely rhizomatous.

All stems ending in an inflorescence, up to ~200 in larger plants; stem pubescence densely overlapping, tufted to appressed stellate hairy, often becoming sparser towards distal end of inflorescence; hairs 164–235 per 2 mm x 2 mm square sampled near base of inflorescence where 2–4 mm wide; stem hairs mostly without stipe, occasionally sparsely short-stiped (0.1 mm), especially distally; stem hair rays 7–24 averaging ~14, rays 0.1–0.2 mm averaging 0.1 mm (rarely a few to 0.5 mm).

Leaves drought deciduous, largest occurring proximally and decreasing in size distally, blade up to 71 mm long and 70 mm wide, abaxial surface paler than adaxial surface due to trichome density; petiole to 41 mm, densely pubescent; leaves orbicular, cordate, and/or deltoid in shape, entire or shallowly to moderately 3–5 lobed, generally entire/wavy to shallowly lobed, base cordate to truncate to slightly cuneate; teeth mostly rounded to broadly-acute, 0.5–4 mm long x 1.5–7 mm wide; rays per hair 5–27 averaging 10–15, rays 0.1–0.5 mm averaging 0.1–0.2 mm; hairs denser on abaxial side of leaf.

Inflorescence of interrupted terminal spikes with flowers clustered in glomerules, occasionally also with proximal axillary spikes, spikes 8–50 cm; glomerules often densely clustered distally; terminal inflorescence glomerules generally 4–12; glomerules composed of 1–43 flowers in clusters of 1–5, each flower subtended by 3 calyx bracts, each flower cluster subtended by 1–5 stipular bracts; glomerules often subtended by leaves and their associated stipules, leaves in inflorescence becoming reduced distally and often absent from more distal glomerules; internodes between glomerules 5–96 mm, generally shorter distally. See Fig. 2E for a dissected glomerule.

Corolla width 21–42 mm; petals 10–20 mm long by 6.5–15 mm wide, asymmetrically obovate with apex rounded, but occasionally truncate or emarginate, pale pink to pink drying pink to pale orange/cream; staminal column 3–7 mm; base of staminal column and corolla lobes simple hairy to only hairy between corolla lobes, base of staminal column occasionally stellate hairy; blooming early April to late December (rarely until March), peak June–August depending on elevation. Later blooms are generally sporadic flowers in the already fruited inflorescence. These later blooms are possibly halted by frost damage in the winter.

Calyx 6–15 mm long, plicate angled in bud; lobes ovate-acuminate, length 3–10 mm, width 2–5 mm, base width 2–4 mm; lobe widest at base to 2.5 mm above base; lobes 1–4× tube; calyx externally with

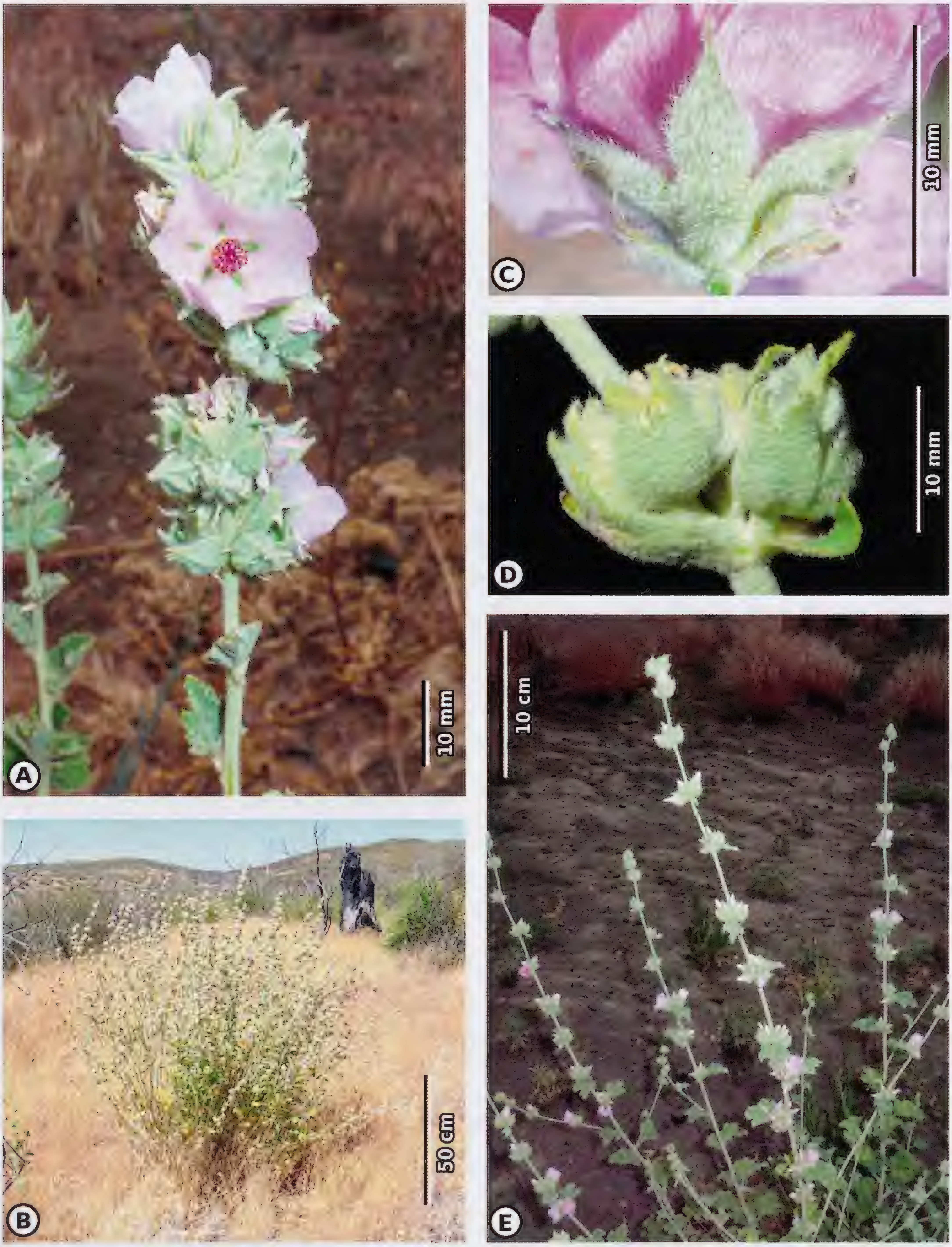

FIG. 8. Representative field photographs of *M. enigmaticus*. A and E. Variation in inflorescence length and compactness. B. Typical full plant. C. Calyx with calyx bracts below. D. Immature glomerule showing stipular bracts with pair of stipules below.

touching to densely overlapping, tufted to appressed, mostly sessile, stellate hairs, generally denser towards calyx base; often with simple multicellular glandular hairs 0.1–0.2 mm, occasionally making inflorescence sticky; stellate hair rays 0.1–2 mm averaging 0.2–0.6 mm; calyx internally (adaxially) densely wavy hairy on the lobes, tube and base of lobes glabrous, hairs 0.1–0.8 mm.

Calyx bracts linear, (3)5–13 mm long by 0.5–1.5 mm wide, longest generally 2/3 to >calyx; stipular bracts ovate, linear, falcate, V-shaped, and/or Y-shaped, 4.5–11 mm long, (0.5)1–8(12) mm wide (width measured at widest point, which may be the distance between the lobe tips for a lobed bract with widely-spreading lobes), simple to 5x irregularly-lobed distally, lobes 0.25–7 mm; stipules 4–10 mm long by 1.5–4 mm wide; calyx bracts, stipular bracts, and stipules tufted to appressed stellate hairy abaxially with rays 0.1–2.3 mm averaging 0.3 mm, adaxially simple wavy hairy similar to calyx interior.

Schizocarp pubescence of deciduous, nonstipitate, tufted stellate hairs at distal end, otherwise glabrous; rays 0.1–0.4 mm, longest near schizocarp center; mericarp oval-shaped with notch at basal attachment, 2.0–2.8 mm x 1.4–1.8 mm; seeds reniform, 1.4–2.0 × 1–1.4 mm, white/tawny-rayed stellate hairs on edges often reduced to golden brown tubercules on seed faces, rays mostly <0.1 mm, mature seed color light to dark brown with purple, red, and/or grey tint; seed coat generally appearing net-veined at 30x magnification.

Paratypes: Latitude, longitude and/or elevation that are estimated from specimen label locality information are indicated with an asterisk (*). See Fig. 1 for a map of localities. USA, CALIFORNIA, **San Diego Co.**: Laguna Mts. Pacific Crest Trail off Sunrise Hwy (S1), about 1 mile from parking area on east side of hwy, 32.915, –116.453, 1700 m, 24-Dec-2005, Bazell 1 (CHSC93162); Drainage from Storm Canyon S-of Vallecito Valley, 32.93450, –116.41524, 665 m, 25-May-2016, Chester 2153 (TBD); Drainage from Storm Canyon S-of Vallecito Valley, 32.93475, –116.41414, 651 m, 25-May-2016, Chester 2154 (TBD); Lower Oriflamme Canyon, 33.00949, –116.50291, 922 m, 25-May-2016, Chester 2155 (TBD); Anza Borrego Desert State Park, Culp Valley Campground, 0.6 m NE of junction of Montezuma Valley Rd (Highway S22) and Public Rd, at Pena Spring, 33.2278, –116.4628, 1009 m, 12-Feb-2009, CRES 480 (SD218779); Anza-Borrego Desert State Park, on Pacific Crest Trail-E of Sunrise Hwy (S1), ca-1 mi SE of its intersection with the road to Lucky 5 Ranch., 32.957, –116.504, 1567 m, 9-Jul-2005, Determan 47 (SD193881); Laguna Mountains, 2 1/2 miles north of Shrine Camp, 32.923*, –116.476*, 1628 m*, 30-Aug-1938, Gander 6395 (SD22606); Laguna Mountains, Desert View, 32.872*, –116.413*, 1850 m*, 31-Aug-1938, Gander 6406 (SD22617); Anza-Borrego Desert State Park-Borrego Palm Canyon, just east of trailhead parking at mouth of canyon., 33.2702, –116.4148, 231 m, 16-Mar-2006, Hendrickson 1250A (SD195245); Anza-Borrego Desert State Park, S fork of Hellhole Canyon, in Culp Valley, N of S 22 (Montezuma Valley Road), 500 meters west of Pena Spring, in the sandy wash on E facing slope, 33.226, –116.470, 1070 m, 6-Oct-2006, Manning 2 (SD193880); Laguna Mountains, 32.91617, –116.46809, 1628 m, 18-Jun-2015, Morse M021 (TBD); Laguna Mountains, 32.91617, –116.46809, 1628 m, 18-Jun-2015, Morse M022 (TBD); Laguna Mountains, 32.91617, –116.46809, 1628 m, 18-Jun-2015, Morse M023 (TBD); Laguna Mountains, 32.91257, –116.46187, 1643 m, 18-Jun-2015, Morse M024 (TBD); Laguna Mountains, 32.91257, –116.46187, 1643 m, 18-Jun-2015, Morse M025 (TBD); Laguna Mountains, 32.91257, –116.46187, 1643 m, 18-Jun-2015, Morse M026 (TBD); Laguna Mountains, 32.90593, –116.45620, 1658 m, 18-Jun-2015, Morse M027 (TBD); Laguna Mountains, 32.90593, –116.45620, 1646 m, 18-Jun-2015, Morse M028 (TBD); Laguna Mountains, 32.90593, –116.45620, 1646 m, 18-Jun-2015, Morse M029 (TBD); Mt-Laguna, 32.87471, –116.41410, 1875 m, 23-Aug-2015, Morse M040 (TBD); Mt-Laguna, 32.87553, –116.41465, 1887 m, 23-Aug-2015, Morse M041 (TBD); Anza Borrego – Culp Valley, 33.20685, –116.48044, 1211 m, 29-May-2016, Morse M060 (TBD); Anza Borrego – Pena Spring, 33.22696, –116.46334, 1018 m, 29-May-2016, Morse M061 (TBD); Anza Borrego – Culp Valley, 33.21352, –116.46206, 980 m, 29-May-2016, Morse M062 (TBD); Anza Borrego – Culp Valley, 33.19982, –116.45392, 1000 m, 29-May-2016, Morse M064 (TBD); Anza Borrego – Culp Valley, 33.19796, –116.45299, 1045 m, 29-May-2016, Morse M065 (TBD); Anza Borrego – Culp Valley, 33.20080, –116.45296, 963 m, 29-May-2016, Morse M066 (TBD); Along PCT near Barrel Spring, south of Montezuma Valley Rd., 33.215659, –116.58756, 1061 m, 22-Jun-2018, Morse M213 (TBD); Montezuma Valley Road west of Ranchita, 33.218518, –116.579386, 1074 m, 22-Jun-2018, Morse M214 (TBD); Monument Peak, Laguna Mts., 32.893*, –116.420*, 1700 m, 20-Aug-1952, Munz 17955 (CAS-BOT-BC203906, RSA78595); Laguna Mountains: Cleveland National Forest; S of Garnet Peak and above Storm Canyon, Penny Pines vicinity, E of Sunrise Highway along the Pacific Crest Trail, 32.9097, –116.4550, 1685 m, 29-Jun-2005, Rebman 12129 (SD174684); Anza-Borrego Desert State Park: Oriflamme Canyon, approx. 3.0 from route S2 on the dirt road into the canyon, 33.0145, –116.4934, 830 m, 14-Mar-2001, Rebman 7148 (SD155153); Laguna Mountains, near the SDSU observatory, 32.840*, –116.427*, 1860 m*, 6-Sep-1987, Reiser s.n. (SD134433); South of Garnet Peak, 32.916*, –116.454*, 1650 m*, 17-Jul-1977, Sproul 157 (RSA388775); Pine Plantation, near Garnet Peak, open gravelly area, 32.915*, –116.458*, 1650 m*, 15-Jul-1977, Sproul 149 (SD114896); At edge of chaparral among Pine Plantation South of Garnet Peak, 32.916*, –116.454*, 1650 m*, 17-Jul-1977, Sproul 157 (DES00029618); Anza-Borrego Desert State Park, E of Ranchita-Culp Valley Camp Jeep Trail, at Pena Spring, north of Highway S22, 33.2250, –116.4625, 1035 m, 19-Oct-2005, Sullivan 128 (SD182280)

EPITHET ETYMOLOGY, PRONUNCIATION, AND COMMON NAME

The epithet refers to the 50+ year enigma surrounding the identity of this taxon. The suggested pronunciation is en-ig-matt'-ick-us (U.S.), or en-eeg-matt'-eek-us (European). The suggested common name is enigmatic bushmallow.

DISTRIBUTION AND HABITAT

Malacothamnus enigmaticus (Malvaceae) is only known from the desert edge of the Peninsular Range in San Diego County, from the San Ysidro Mountains in the north to the Laguna Mountains in the south.

Whether *M. enigmaticus* exists farther to the south, in Baja California, is currently unknown. Four specimens from just south of San Diego County in Baja California, Mexico are similar to *M. enigmaticus*, but are disjunct from the San Diego County populations and do not cluster well with the others in the PCAs. Additional specimens and further research are needed to determine the identity of the Baja California plants.

Malacothamnus enigmaticus is the only *Malacothamnus* species in its geographic range, with *M. densiflorus* found in the cismontane area to the west and *M. fasciculatus* found in the San Jacinto / Santa Rosa Mountains to the north. Along the ~90 km north-south boundary between *M. densiflorus* and *M. enigmaticus*, we found only one location with any possible-hybrid specimens which will be investigated further in the future. Two disjunct plants of *M. fasciculatus* have been found along the creek in Coyote Canyon northwest of Borrego Springs and are presumably wash-downs from the Santa Rosa Mountains. The geographic range of *M. enigmaticus* and the other *Malacothamnus* species in the surrounding area is shown in Fig. 1.

Because *M. enigmaticus* is a strict fire follower, it is more difficult to pin down its distribution compared to non-fire following species. While some sparse plants were found to persist in sites 14 and 18 years post-fire, in other sites the plants were all or mostly dead just three years post-fire. The current distribution is based on historic herbarium specimens and field surveys from 2013–2017. Future fires will likely reveal additional plants in the distribution gaps and possibly somewhat expand the distribution boundaries.

Malacothamnus enigmaticus is found almost entirely on the desert side of the mountain crest. The only specimens west of the crest are in the Laguna Mountains, all of which are within just 0.5 km of the crest. The main known concentrations are in the upper alluvial fan of Cottonwood Canyon at ~900 m; the eastern slopes of Chariot Canyon at ~1200 m; the flattish area at the Laguna Mountain Crest from Mount Laguna to Garnet Peak at 1600–1900 m, and in the bouldery area from just east of Ranchita to Culp Valley at 900–1300 m. There may be populations on the steep desert slopes of the Lagunas, but if so, they are currently unknown due to difficult terrain and access.

There are wash-down specimens at elevations as low as 230 m, from seeds brought there by sediment flows after fires at higher elevations, evidenced by specimens growing in deposited mud. Wash-down specimens in Indian Canyon near Collins Valley northwest of Borrego Springs indicate that there must be a population at higher elevations in the Los Coyotes Indian Reservation east of Hot Springs Mountain. Unfortunately, that area has restricted access and few voucher collections of any plant taxon, so we cannot delineate its range there. We have placed a question mark at this location in Fig. 1.

Malacothamnus enigmaticus occupies a unique habitat in San Diego County, geographically separated from similar habitat to the north and south, where montane elevations transition rapidly to the low desert on the east (Fig.1). This unique habitat may have contributed to the speciation of *M. enigmaticus*.

To the south of its range, montane elevations disappear. To the north of its range, the montane regions are not in as close proximity to low desert elevations and are oriented differently with respect to the low desert. The Santa Rosa Mountains are a ridge extending into the desert, with desert on both sides. The low desert next to the San Jacinto Mountains is mostly in a different orientation, to the northeast of the montane elevations instead of almost directly east. Only *M. densiflorus* and *M. fasciculatus* have been found in these adjacent areas.

Malacothamnus enigmaticus grows in a wide range of vegetation communities, slopes, aspects, and soil moistures. The only clear site preference is a recent burn area in full or nearly-full sun. At lower elevations, where it is warmer and drier, plants are more common near springs, washes, and bouldery north-facing slopes.

Due to the wide range of habitats, many associated species were observed. The most commonly-observed associates include *Artemisia ludoviciana* Nutt., *Bromus madritensis* subsp. *rubens* (L.) Husn., *Bromus tectorum* L., *Ceanothus palmeri* Trel., *Ceanothus perplexans* Trel., *Cercocarpus betuloides* var. *betuloides* Nutt., *Eriogonum fasciculatum* var. *polifolium* (Benth.) Torr. & A.Gray, *Prunus ilicifolia* var. *ilicifolia* (Nutt. ex Hook. & Arn.) D.Dietr., *Quercus cornelius-mulleri* Nixon & K.P.Steele, and *Sambucus nigra* subsp. *caerulea* (Raf.) R.Bolli. However, these are not consistently observed at all sites.

CONSERVATION STATUS

Malacothamnus enigmaticus is a rare species, known from just two areas separated by a gap of ~15 km, one in the Laguna Mountains and one in the Pinyon Ridge / Culp Valley / San Ysidro Mountain area. For each of those areas, the minimum polygonal area enclosing all known plants has an area of 120 to 130 km^2. The maximum area enclosing all known plants and surrounding unexplored habitat that appears to be suitable for this species is not much greater for the Laguna Mountains population, but could be as high as 300 km^2 for the Pinyon Ridge / Culp Valley / San Ysidro Mountain population due to the unknown extent in the Los Coyotes Indian Reservation area.

The known populations are ~3000 plants in the Laguna Mountains and ~500 plants in the Pinyon Ridge / Culp Valley / San Ysidro Mountain area. The low rainfall years after the burns in these areas might have limited the numbers. Additional plants are likely in areas not recently burned or with access limitations.

Most known plants are within Anza-Borrego State Park, Cleveland National Forest, and Bureau of Land Management (BLM) property currently managed for conservation and recreation.

Threats to the species include development, fire suppression, chemical and/or mechanical post-fire vegetation suppression, and possibly fires occurring multiple years in a row which could deplete the seed bank. All of these threats appear minimal at this time.

Considering the limited distribution and relatively small number of plants with a low degree of threat, we propose a California Rare Plant Rank of 1B.3 for *M. enigmaticus*. "Plants with a California Rare Plant Rank of 1B are rare throughout their range with the majority of them endemic to California" (CNPS, 2017). A threat rank of .3 indicates the taxon is "Not very threatened in California (less than 20% of occurrences threatened / low degree and immediacy of threat or no current threats known)" (CNPS, 2017).

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APPENDIX 1

KEY TO CATEGORICAL MEASUREMENTS

Number of flowers per node

1 = 1–3

2 = 4–9

3 = 10+

Distance from tip of calyx lobe to where the lobe is 1.0 mm wide

1 = <1 mm

2 = 1–2 mm

3 = >2 mm

Leaf/calyx hair density

0 = None

1 = Very sparse, could be scattered throughout, but generally not near similar hairs

2 = Scattered throughout and near similar hairs, but most not touching each other (exception may be the sparse but long-rayed hairs on *M. densiflorus*)

3 = Most touching/overlapping, but can be easily seen through them

4 = Densely overlapping, little can be seen through them

5 = Solid – nothing can be seen through them

Hair color presence (tawny-yellow or white)

0 = No

1 = Yes

Appendix 2 List of Measured Characteristics with Principal Component Analysis (PCA) Loadings

	Component Loadings for *M. enigmaticus* / *M. fasciculatus*		Component Loadings for *M. densiflorus* / *M. enigmaticus*	
Measured characteristic	PCA1	PCA2	PCA1	PCA2
# flowers per node min	0.09	0.03	0.01	0.04
# flowers per node median	0.08	0.10	−0.05	0.06
# flowers per node max	0.03	0.19	−0.05	0.04
Infl branch length min (mm)	0.04	0.29	0.16	0.14
Infl branch length max (mm)	−0.06	0.31	0.03	0.02
Infl internode length max (mm)	0.14	0.04	0.11	0.03
Stem thickness just below proximal infl node (mm)	0.14	0.14	−0.01	0.15
Stem thickness just above proximal infl node (mm)	0.11	0.13	−0.01	0.15
Stem thickness near distal-most infl node (mm)	0.15	−0.08	−0.09	0.15
Stem stellate hairs per 2 × 2.3 mm square	0.13	0.16	−0.18	0.22
Stem stellate hair ray longest (mm)	−0.06	−0.21	0.20	−0.03
Stem stellate hair ray shortest (mm)	0.01	−0.02	0.09	−0.18
Stem stellate hair ray average (mm)	−0.11	−0.23	0.20	−0.18
Stem stellate hair stipe longest (mm)	−0.12	−0.23	0.11	−0.19
Stem stellate hair stipe shortest (mm)	-	-	0.00	−0.03
Stem stellate hair stipe average (mm)	-	-	0.15	−0.19
Stem simple glandular hairs shortest (mm)	-	-	0.14	−0.02
Stem simple glandular hairs longest (mm)	-	-	0.15	−0.04
Stem simple glandular hairs average (mm)	-	-	0.13	−0.07
Stem stellate hairs tawny-yellow	-	-	−0.03	0.05
Stem stellate hairs white	0.09	0.03	−0.07	0.14
Calyx length min of 3 flowers (mm)	0.22	0.03	0.21	0.18
Calyx lobe length min of 3 flowers (mm)	0.22	0.07	0.21	0.19
Calyx lobe width min of 3 flowers (mm)	0.12	−0.19	0.05	0.12
Distance of widest part of calyx lobe from lobe base, min of 3 flowers (mm)	0.19	0.01	0.00	0.16
Distance from tip of calyx lobe to where the lobe is 1.0 mm wide, min of 3 flowers[2]	0.18	0.09	0.20	0.06
Calyx length max of 3 flowers (mm)	0.22	0.01	0.21	0.19
Calyx lobe length max of 3 flowers (mm)	0.23	0.05	0.21	0.20
Calyx lobe width max of 3 flowers (mm)	0.17	−0.15	0.08	0.13
Distance of widest part of calyx lobe from lobe base, max of 3 flowers (mm)	0.20	−0.03	−0.02	0.20
Distance from tip of calyx lobe to where the lobe is 1.0 mm wide, max of 3 flowers	0.18	0.19	0.16	0.01

APPENDIX 2 CONTINUED

	Component Loadings for *M. enigmaticus* / *M. fasciculatus*		Component Loadings for *M. densiflorus* / *M. enigmaticus*	
Measured characteristic	PCA1	PCA2	PCA1	PCA2
Calyx length average of 3 flowers (mm)	0.23	0.02	0.21	0.19
Calyx lobe length average of 3 flowers (mm)	0.23	0.07	0.21	0.20
Calyx lobe width average of 3 flowers (mm)	0.16	−0.18	0.08	0.15
Distance of widest part of calyx lobe from lobe base, average of 3 flowers (mm)	0.21	−0.02	−0.01	0.21
Distance from tip of calyx lobe to where the lobe is 1.0 mm wide, average of 3 flowers	0.19	0.17	0.20	0.05
Calyx bract length shortest (mm)	0.22	−0.11	0.20	0.15
Calyx bract length longest (mm)	0.21	−0.09	0.21	0.14
Calyx bract widest part min (mm)	0.12	−0.09	−0.07	0.15
Calyx bract widest part max (mm)	0.14	−0.19	−0.12	0.14
Calyx bract margin longest hairs average length (mm)	0.14	−0.15	0.22	−0.02
Calyx hair rays longest (mm)	0.15	−0.21	0.23	−0.06
Calyx lobe hair density	−0.01	0.07	−0.17	0.16
Stipular bract width min (mm)	0.20	−0.05	−0.12	0.21
Stipular bract width max (mm)	0.20	−0.04	−0.14	0.23
Distal leaf hair density upper surface	0.03	−0.28	−0.10	0.06
Distal leaf hair density lower surface	0.07	−0.13	−0.15	0.19
Proximal leaf hair density upper surface	0.01	−0.17	−0.08	0.04
Proximal leaf hair density lower surface	0.04	−0.05	−0.12	0.18

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CALFLORA: TOOLS FOR THE 21ST CENTURY PLANT LOVER

For 20 years, the 501(c)3 non-profit Calflora Database has been providing information about California plant biodiversity for use in education, research, and conservation. Every plant taxon that grows wild in California will be found within Calflora, a list of more than ten thousand species (including parent species). The taxonomic coverage parallels that in TJM2 (Baldwin et al. 2012). For each species, there is a taxon report page, which includes the scientific name and author(s), common name(s), alternate name(s), plant status (native or not), family, flowering months (where relevant), reference photos of species, habitat, communities, and its distribution seen on a map of the state. These resources are available for free through the Calflora website (https://www.calflora.org/).

Here's an example of the distribution of *Clarkia concinna* (Fischer & C.Meyer) E.Greene (Red ribbons) (Fig. 1A); each blue dot represents an observation of this species. *Clarkia concinna*, a dicot, is an annual herb that is native and endemic to California. The presence of the plant in a watershed is considered *confirmed* if there are two or more observations in the watershed. The presence of the plant in a watershed is considered *possible* if there is a single observation in the watershed.

Hayley Ross observed this *Clarkia*, took a photo, and submitted her observation including photo to Calflora (Fig. 1B). Calflora data contributors may opt to fill in multiple fields, including phenology, habitat, and number of plants. The only mandatory fields in Calflora when entering plant data are species, location, date, and observer name. Ross chose to publish her record and specific location to make it viewable to other Calflora users; rare plant observers may choose to obscure their locations. Ross also chose a Creative Commons license allowing non-commercial use of her photo.

If a Calflora user questions the plant identity of a given Calflora observation, or has another comment on an observer's record, every Calflora observation includes a comments field. Comments are viewable on every published observation. This allows for a public discourse that becomes part of the observation.

Plant species names change over time. To ease this pain, Calflora crosswalks (yes, a verb) those 30,000 names so the user may find the species by searching by any synonym.

Some Calflora observations include one or more photos. Many of the better photos are used as reference photos on Calflora taxon report pages. While choosing the best reference photos is performed by a dedicated team of Calflora volunteers, Calflora relies on seven staff and contractors to maintain this powerful database. Various web applications such as What Grows Here, Observation Hotline, and the Planting Guide allow users to comb through millions of records by queries according to their interests.

With now over 1.6 million plant observations entered directly into Calflora, as well as serving another 70,000 from iNaturalist and 1.57 million from the California Consortium of Herbaria, users may explore these troves of plant observations to create illustrated plant lists for hiking and load the observations onto Calflora's Observer Pro smartphone app to find historical plant populations, create new assessments, and track changes to plant populations over time.

Calflora also contains soil and climate information for the state, which informs a Planting Guide algorithm. Users seeking a list of natives that will grow well at a specific location may also filter the query by riparian, shady, and omit plants at the edges of their tolerances. Users may also generate lists of locally rare or potentially extirpated plants for specific areas, and travel to those places to search for them.

Using What Grows Here, plant lovers may use the protected areas layer above the map "Layers" or draw a polygon around a favorite botanical hotspot. After filtering for "native species" or "date", users can produce a list of species that grow in a specific location. One may further filter for just "non-natives", or to include or exclude "surveys and checklists".

To maintain this valuable resource and its many applications, seven Calflora staff and contractors are needed. These include JAVA developers for the database development and maintenance, smartphone application developers, as well as specialists in outreach, education, and communication. Calflora's JAVA developer John Malpas has been building out the database structure since he started in 2003, and Calflora's Executive Director Cynthia Powell received her M.S. in GIS Geographic Information Science (GIS) in 2010 and joined the team in 2013. While the rest of the team is based in northern California, Calflora's Communications and Outreach Director Michelle Tollett is based in southern California where she leads hikes and trainings emphasizing the southern half of the state.

Because Calflora depends on plant observations from its users, there is a Calflora data collection smartphone app called Observer Pro for use while hiking and in the field (no data plan or connectivity

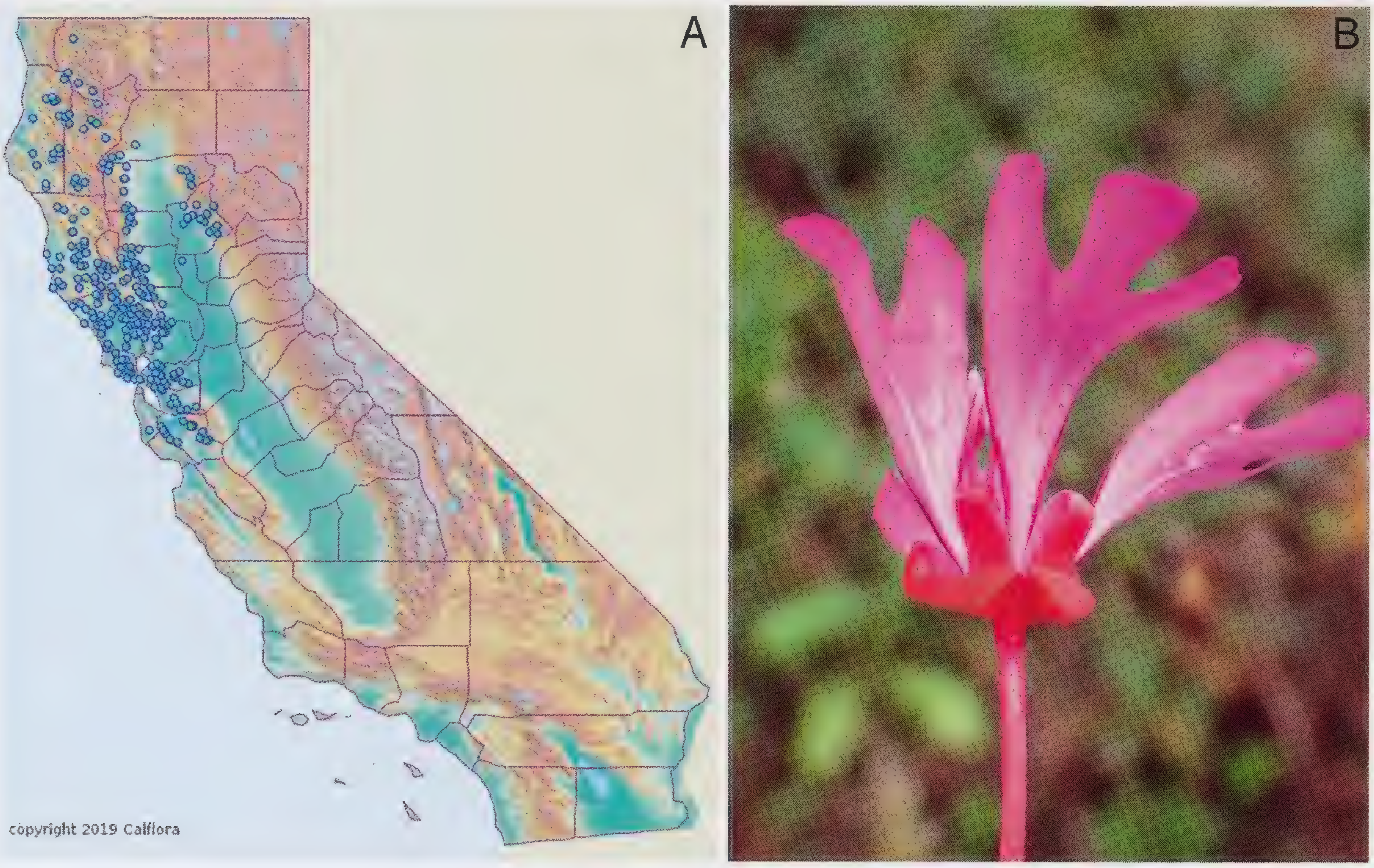

FIG. 1. (A) Calflora's distribution map of *Clarkia concinna*. Blue dots represent an observation of this species. (B) A *Clarkia concinna* flower. Photo: Hayley Ross (CC BY-NC 4.0).

FIG. 2. Madena Asbell and Tom Kayne on a Calflora Observer Pro hike looking at *Tetradymia* sp. in Joshua Tree National Park May 2019. Photo: Lynn Sweet.

needed). Users may also find customized data collection forms on this app, such as a postfire form, to track restoration and plant recovery after a fire. Agencies using Calflora to track changes in invasive plant populations may also design their own customized data collection forms; these fields inform the reports generated by Calflora's Weed Manager system.

Calflora presentations and Calflora Observer Pro hikes are happening now across the state (Fig. 2). To set up yours, contact Calflora (spprt@calflora.org).

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